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ARCHAEOZOOLOGICAL, TAPHONOMIC AND ZOOMS INSIGHTS INTO THE PROTOAURIGNACIAN FAUNAL RECORD FROM RIPARO BOMBRINI

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ABSTRACT

Human adaptation to climatic variations is being discussed at different scales and from diverse perspectives and specializations in Paleolithic archaeology. We suggest examining human mobility on the local scale through the faunal record to better understand human-environmental interactions during the early dispersal of anatomically modern humans along the Mediterranean coast. Riparo Bombrini is located in the renowned Balzi Rossi complex in Northwest Italy. The site offers an excellent opportunity to compare two distinct Protoaurignacian levels yielding well-documented and well-dated deposits. Previous studies of spatial, lithic, and raw material data from these two Protoaurignacian levels have revealed distinct mobility signatures as well as undeniable evidence for the resilience of the Protoaurignacian technocomplex during episodes of climatic instability including the HE4 event, circa 40ka cal BP. The highly fragmented nature of the animal bones at the site warrants the application of the ZooMS (Zooarchaeology by Mass Spectrometry) collagen fingerprinting technique. For this research we carried out taphonomic and archaeozoological analyses with integrated systematic ZooMS using a mass sampling strategy. The results suggest stability in hunting strategies over time in spite of the apparent shift in mobility strategies from level A2 to level A1 at Riparo Bombrini.

KEYWORDS

Protoaurignacian, Early Upper Palaeolithic, hunting strategies, Paleolithic archaeozoology, taphonomy, ZooMS, Riparo Bombrini, Italy

1 Introduction

The Protoaurignacian technocomplex has long been thought to be one of the earliest cultural manifestations associated with the dispersal of anatomically modern humans along the Mediterranean coast. Numerous debates are still ongoing about the origin and the nature of the Protoaurignacian in Western Europe. Surprisingly, despite the relevance of subsistence to understand mobility strategies, complete and detailed archaeozoological analyses are very rare for Protoaurignacian or coeval assemblages (including other denominations such as Archaic Aurignacian, Aurignacian 0, Initial Aurignacian, etc.) (Pike-Tay et al., 1999; Soulier, 2013, 2014). This implies that early anatomically modern humans' mobility and land use strategies associated with Protoaurignacian assemblages in Western Europe have largely been discussed on the basis of the information available from lithic technology and raw material procurement alone. To the extent that they are presented, archeozoological data have mainly been used to provide some degree of environmental context or baseline information on subsistence strategies, with little attention paid to other behavioral dimensions they can shed light on (Porraz et al., 2010; Tomasso and Porraz, 2016; Brugal et al., 2017; Riel-Salvatore and Negrino, 2018a; Holt et al., 2019). However, it is now well established that faunal resources can hold a determinant place in hunter-gatherer's technological changes and mobility strategies (Gaudzinski and Roebroeks, 2000; Burke, 2006a, 2006b; Costamagno et al., 2006; Gaudzinski, 2006; Delagnes and Rendu, 2011; Niven et al., 2012; Rendu et al., 2012).

To support the traditionally accepted eastern origin of the Protoaurignacian, the technocomplex has been argued to have similarities to assemblages in Bulgaria (Kozarnika, Tsanova et al., 2012), Crimea (Siuren-I, Demidenko and Otte, 2000; Demidenko and Noiret, 2012) and SW Russia (Kostenki 17/II, Dinnis et al., 2019), as well as to the Levantine Ahmarian technocomplex (Mellars, 2006). However, recent dates indicate that the earliest instance of the Protoaurignacian is documented at the site of Isturitz, in SW France (Barshay-Szmidt et al., 2018), supporting a potential indigenous origin for the technocomplex in western Europe (Anderson et al., 2015; cf. Kadowaki et al., 2015). This could also help explain early dates for this industry in other Western European sites and support a mosaic conceptualisation of the Middle-Upper Paleolithic

transition (Guy Straus, 2005; Clark and Riel-Salvatore, 2009; Maíllo-Fernández and de Quirós, 2010). It is important to highlight that, in all cases where the two industries have been documented at the same site, the Protoaurignacian underlies the Early Aurignacian. Furthermore, while some scholars argue for a general homogeneity of the Protoaurignacian, recent work on this technocomplex has shown to display a heretofore underappreciated degree of internal variability, at least some of which appears to be correlated to changes in overall mobility strategies (Falcucci et al., 2017, 2018; Riel-Salvatore and Negrino, 2018a, 2018b). Thus, while debate continues as to whether it represents a southern European manifestation of a larger "Aurignacian" phenomenon that is represented in other parts of the continent by the Early Aurignacian, overall, it appears that the Protoaurignacian represents a distinct adaptation and technocomplex.

In order to contribute to ongoing discussions about the internal variability of the Protoaurignacian as a technocomplex, this paper presents an analysis of faunal remains from the two Protoaurignacian levels at the site of Riparo Bombrini (Liguria, NW Italy). We start by introducing the record from Riparo Bombrini as a case study, summarising the latest data published over the past few years and introducing its faunal collections as an important vector of information that has much to contribute to the ongoing discussions. One of the principal challenges that emerge is the highly fragmentary nature of the faunal remains from the site, which creates some particular difficulties in its analysis. A combination of archaeozoological, taphonomic, and Zooarchaeology by Mass Spectrometry (ZooMS) analyses prove to be a suitable and innovative methodological solution to this context, and its results are presented in the following section. The paper closes with a discussion that situates these new data in the context of the debate about the internal variability of the Protoaurignacian and highlights how the integration of faunal and other archaeological data is essential to shedding much-needed light on the cultural adaptations of Early Upper Paleolithic foragers in Europe beginning roughly 42,000 years ago.

1.1 Previous Work on the Protoaurignacian at Riparo Bombrini

Located in NW Italy in the storied Balzi Rossi site complex located immediately east of the border with France, Riparo Bombrini is a rockshelter of which a small part survives today (Fig. 1). The construction of the Genoa-Marseille railroad in the late 19th century used explosives to blast through part of the Balzi Rossi and truncated the talus deposit originally present in front of Grotta del Caviglione, the eastern edge of which is known today as Riparo Bombrini. A first testing in 1938 (Cardini, 1938) was followed by a limited excavation in 1976 (Vicino, 1984) and controlled excavations from 2002-05 (Holt et al., 2019). Since 2015, the site has been under excavation by two of the authors, with the stated aim of clarifying the timing and cultural dynamics of the Middle-Upper Paleolithic transition at one of the rare sites to have yielded diagnostic *Homo sapiens* remains in Protoaurignacian context (Negrino and Riel-Salvatore, 2018; Riel-Salvatore and Negrino, 2018a, 2018b).

These prior excavations have revealed that the site comprises very recent (42-45 ky cal BP) Late Mousterian deposits overlain by three Protoaurignacian levels spanning the interval 42ky-36ky cal BP (Fig. 2) (Higham et al., 2014; Benazzi et al., 2015; Holt et al., 2019). While an erosional disconformity separates the two technocomplexes, they do not appear to be separated by a significant time gap (Riel-Salvatore and Negrino, 2018a). The site's chronology broadly corresponds to that documented at nearby Riparo Mochi, which represents the western edge of the Caviglione talus discussed above (Fig. 1)(Kuhn and Stiner, 1998; Douka et al., 2012).

One of the most striking elements to come out of prior work at Riparo Bombrini is that the Protoaurignacian levels, in spite of showing considerable lithic technotypological homogeneity (see Bertola et al., 2013), clearly document differences in mobility strategies and land-use patterns, with Level A1 showing a residential mobility strategy while Level A2 shows a logistical mobility strategy (Riel-Salvatore, 2007, 2010). These differences are accompanied by differences in the production of bladelets and appear to correspond to adaptations to changing paleoenvironmental conditions (Riel-Salvatore and Negrino, 2018a), which testify to the fact that Protoaurignacian technocomplex was a

flexible one that permitted a great deal of resilience in forager behavior across even dramatic paleoclimatic shifts including that corresponding with the eruption of the Phlegrean Fields ca. 39ky cal BP (Riel-Salvatore and Negrino, 2018b).

Overall, micromorphology, pollen, faunal and microfaunal data published in Holt et al. (2019) associate Level A2 with a phase of climatic degradation that could correspond to just after Glacial Interstadial 9 (GI 9), dated around 40.2 ky cal BP (Rasmussen et al., 2014), and extend through the climatic instability associated with HE4 (~39.85±0.14ky to 38.2ky cal BP according to Giaccio *et al*. (2017)). In contrast, Level A1 is associated with slightly more temperate and mesic conditions (Arobba and Caramiello, 2009; Riel-Salvatore and Negrino, 2018a; Holt et al., 2019), lasting from around 38 to 36 ka cal BP (Riel-Salvatore and Negrino, 2018b; Holt et al., 2019) which could correspond to Glacial interstadial 8 (GI8) according to the climato-stratigraphy detailed in Rasmussen et al. (2014).

Riparo Bombrini's Protoaurigacian Levels A1 and A2 are dense in remains of various kinds, especially lithics and faunal remains, and they also include features including *cuvette*-type hearths and pits. However, to date, only the Mousterian levels have benefited from a formal spatial analysis (Riel-Salvatore et al., 2013), which revealed that the site's Neanderthal occupants had distinct activity areas when they occupied it and that the positioning of these varied according to their overall mobility strategies. Given similarities in hearth placement in Levels A1 and A2 and in the Mousterian, the same may also have been true during the Protoaurignacian at the site. The presence of a potential third Protoaurignacian level is limited to a narrow band of deposits along the back wall of the shelter; these deposits likely represent a level that was largely eroded away and, due to its low artifact and faunal content and very limited spatial extent, it will be disregarded in the present analysis.

One of the outstanding questions about Protoaurignacian variability at Riparo Bombrini, and indeed much of the Protoaurignacian as a whole, is how faunal data fits into the equation (Pike-Tay et al., 1999; Soulier, 2013, 2014; Anderson et al., 2015; Falcucci et

al., 2017). By way of reference within the Balzi Rossi, at Riparo Mochi, the Protoaurignacian lithic assemblages have so far always been studied as a whole, thus masking potential variability within this industry at this site (e.g., Kuhn and Stiner, 1998; but cf. Grimaldi et al., 2014). Likewise, data on the large mammal assemblage have either been overlooked (Kuhn and Stiner, 1998), or presented for level G as a whole, which is associated with the highest frequency of roe deer in the Mochi sequence, although red deer is also abundant (Alhaique et al., 2004; Berto et al., 2019). In a recent study of bone and antler technology at Mochi, Tejero and Grimaldi (2015, p. 68) also make passing reference to the fact that "long bones were systematically fractured for bone marrow extraction and consumption" without providing detailed data in support of this observation. Recently published microfaunal data from Mochi indicate that its transitional levels are associated with "two cold and one slightly warm oscillations […] depicting a forest and bush reduction near the shelter"(Berto et al., 2019, p. 21), but again all the material for level G was studied as a whole, making finer-grained interpretations impossible. The same is also true of analyses of mollusk procurement (Stiner et al., 2000).

The situation is somewhat better at Bombrini, where faunal data (in this case species abundance) has been reported from the various levels at the site. Holt et al. (2019, Table 4) suggest that the species composition of the faunal assemblages from Riparo Bombrini indicates that the Protoaurignacian was accumulated under slightly colder conditions than the Late Mousterian, as shown by the higher frequency of bovids, mountain goats (*C. ibex*) and chamois (*R. rupicapra*) in those levels. As well, identified remains of rhinoceros and equids in Level A2 imply the presence of an open plain ecosystem between the base of the cliffs of the Balzi Rossi and the lower-lying Tyrrhenian Sea at that time. From a behavioral perspective, no taphonomic or skeletal element representation data have been published to date, but it is worth highlighting here the high degree of fragmentation of the Protoaurignacian faunal assemblages: only 1.82% (of 3842 bone fragments) and 0.87% (of 4245 fragments) of all animal bones could be identified in Levels A1 and A2, respectively (Holt et al., 2019, p. 5), in spite of these assemblages being more than an order of magnitude larger than in the Late Mousterian

(average number of bone fragments = 442, avg % identified = 2.26%). Seeing how most of the identifications reported in Holt et al. (2019) are generally based on teeth, it seems warranted to say that the Protoaurignacian faunal record at Riparo Bombrini is both more abundant and more fragmented than in the underlying levels, which hints at the fact that a distinct suite of taphonomic processes was at work in those levels compared to the Late Mousterian. The exact nature of these processes, their relevance to understanding variability in human behavioral strategies during the Protoaurignacian, whether they co-vary in any meaningful way with documented shifts in mobility strategies and lithic technology, remain a series of important open questions, however.

1.2 Evidence of Mobility Strategies in Fragmented Paleolithic Faunal Assemblages Enhanced by ZooMS Collagen Fingerprinting

In his forager/collector models, Binford (1980) documented a spectrum of behaviors in which he ultimately describes two opposite types of mobility patterns (i.e. residential vs logistical) that are still widely used in Paleolithic archaeology to discuss human dispersals and land-use patterns from a Human Behavioral Ecology perspective (Kelly, 1995; Clark and Riel-Salvatore, 2006; Schulting et al., 2008; Andrefsky, 2009; Delagnes and Rendu, 2011; Riel-Salvatore and Negrino, 2018a, 2018b; Lugli et al., 2019; Moncel et al., 2019; Wißing et al., 2019). Binford originally developed his models within a Middle Range theoretical framework to distinguish opposite types of mobility through the identification of different types of site (residential mobility: base camp and localities; logistical mobility: base camp, field camp, station, and storage cache). However, a strict definition of the models is rarely applied today to avoid reductionist logic. In this paper, we are specifically interested in Binford's (1980) discussion of hunter-gatherer resource management. While hunter-gatherers with a residential mobility "map onto" the existing environment and adapt the way they acquire resources (e.g. food, raw material) to external constraints, hunter-gatherers with a logistical mobility adapt their subsistence strategies in specializing on a critical resource (e.g. lithic raw material, migratory preys) that would otherwise limit mobility. From an archaeological perspective, this distinction provides theoretical grounds to discuss the variability in resource management perceptible through the lithic record (raw material selection, lithic *chaîne opératoire*,

256 reduction sequences, and tool maintenance) and the faunal record (prey selection, carcass
257 transport, and carcass treatment). For instance, Delagnes and Rendu (2011) developed an
258 approach that demonstrated a link between the transportability attributes of the different
259 lithic technological systems (as potential mobility proxies) with the nature of the faunal
260 assemblages stratigraphically associated to those systems. They were able to link faunal
261 assemblages dominated by non-migratory species (e.g. red deer, roe deer) to lithic
262 technological systems with a low potential for group mobility (higher duration of
263 reduction sequences, single purpose end-products with short use-life). Conversely,
264 technological systems with high mobility potential (high versatility of blanks, long use-
265 life, low investment in core preparation) were associated with faunal assemblages
266 dominated by gregarious migratory species with predictable seasonal moves (e.g.
267 reindeer).
268
269 In our study, we further explore the potential proxies for mobility strategies within the
270 faunal record, specifically in terms of resource management. To do so, we selected three
271 proxies for resource management that will be explored in the Protoaurignacian faunal
272 record of Riparo Bombrini, namely prey selection, carcass transport, and carcass
273 treatment. On a basecamp such as Riparo Bombrini, those three resource management
274 proxies allow us to first discuss whether hunter-gatherers adopted a more generalist prey
275 selection strategy, exploiting a breadth of available prey species in the environment
276 surrounding the site, or if they specialized on a single gregarious migrating species,
277 which would imply a higher degree of mobility and logistical planning (Brugal, 1999;
278 Grayson and Delpech, 2002; Mellars, 2004; Costamagno et al., 2006; Gaudzinski, 2006;
279 Rendu et al., 2012). Second, carcass transport reconstruction helps us assess whether
280 animals were hunted on a local scale and brought back whole to be processed at the site
281 or if the animals were hunted far from the site and therefore first butchered at the kill site
282 (Lyman, 1985; O'Connell et al., 1988, 1990; Grayson, 1989; Lupo, 2001; Marean and
283 Cleghorn, 2003; Faith and Gordon, 2007). And third, carcass treatment is generally
284 discussed in terms of exploitation intensity measured either by the frequency of cut marks
285 present on skeletal remains (see Domínguez-Rodrigo and Yravedra, 2009 for a good
286 literature review) or the exploitation of bone marrow and bone grease (Outram and

Rowley-Conwy, 1998; Outram, 2001; Stiner, 2002a; Munro and Bar-Oz, 2005; Outram et al., 2005; Morin, 2007; Costamagno, 2013; Costamagno and Rigaud, 2013; Morin and Soulier, 2017). The intensification of carcass processing is often seen as occurring hand-in-hand with increasing diet breadth as an adaptive response to external constraints such as environmental instability and demographic changes (Grayson and Delpech, 1998; Stiner et al., 2000; Stiner, 2002a; Stiner and Munro, 2002; Morin et al., 2019). However, measuring the intensity of carcass exploitation using only one of these criteria can easily be misleading. The interpretation of cut mark frequencies for instance has been widely criticized because of the numerous taphonomic and cultural factors influencing those frequencies including fragmentation, butchery practices, carcass size, butchering tool types, and so on (Domínguez-Rodrigo and Yravedra, 2009). Another example is provided by the fact that specific skeletal elements can be considered good raw material for the confection of tools while others are not. In the same way, the grease contained in cancellous bones can be exploited in different ways depending on whether it is used as a source of food or a source of fuel.

The intensity of carcass exploitation has recently been studied conjointly with lithic techno-economic patterns to discuss curation and mobility strategies (Costamagno et al., 2006; Costamagno, 2013). We adopt a similar approach, borrowing the concept of curation from lithic analysis (see Andrefsky, 2009) in order to evaluate the degree of carcass curation defined as the process reflecting a carcass's actual exploitation at the base camp relative to its maximum physical utility, or potential for exploitation. The maximum physical potential exploitation implies extracting all possible resources on the carcass, including skin, tendons, meat, bone raw material, marrow and most importantly the grease contained in cancellous bones. Following this logic, a highly curated carcass does not imply that all those resources were intensively exploited, but it reflects the array of choices potentially made by hunter-gatherers to exploit some resources that will result in the exhaustion of all exploitable resources on a single carcass.

On a methodological perspective, prey selection and carcass transport can be assessed with traditional quantitative units used in archaeozoology, such as the Number of

Identified Specimens (NISP) combined with the Minimum Number of Individuals (MNI) to evaluate the diversity of animal species exploited on the site, and measuring the Minimum Number of Elements (MNE) and skeletal representation to evaluate what carcass parts were brought back to the base camp for each exploited species (Grayson 1984; Marean et al. 2001; Lyman 2008; Morin et al. 2016). Of course, those measurements must be combined with taphonomic analyses to ensure that the animal carcasses under consideration were indeed exploited by humans instead of other potential carnivores (e.g., wolves or hyenas). Carcass treatment, on the other hand, can be discussed by combining archaeozoological and taphonomic analyses and should include recording the nature of fragmentation from the indeterminate fraction of the faunal assemblage. If one can discriminate between the different post-depositional taphonomic effects that can fragment faunal remains such as carnivore action, animal and human trampling, deposit compaction, water action, and bioturbation, it is then possible to identify some anthropic fragmentation effects (if not masked by the extent of the post-depositional effects): tool manufacture (surface alterations), cooking, marrow and grease exploitation, and burning for fuel. As will be seen below, these last two behaviors were of special interest at Riparo Bombrini in the concept of carcass curation.

The sequence of activities leading to bone marrow and grease exploitation would start with the first known steps of animal exploitation : killing the animal, butchering it (cut marks, scraping marks for skinning, dismembering, filleting, etc.) and possibly processing some skeletal elements for craft purposes (manufacturing traces; grooving, polish, unfinished or broken bone tools). Marrow extraction alone implies the deliberate fracturing of long bone shafts to recover the cold marrow. This action typically produces numerous shaft fragments bearing dynamic impact fractures and bone flake removals (or splintering) around the area where the fresh bones were cracked open (Outram 2001; Munro and Bar-Oz 2005; Vehik 1977; Manne 2012). Finally, grease exploitation entails further carcass processing starting with the breakage of cancellous bones which is defined as grease processing by Morin and Soulier (2017), and potentially the boiling or heating of the crushed cancellous bones (grease rendering). In the case of grease rendering, a choice can be made between appendicular or axial bones at this point as they produce

different types of grease (Wilson, 1924; Vehik, 1977; Binford, 1978; Outram, 2001). Archaeological evidence of grease rendering would therefore include comminuted cancellous bones to extract the grease and traces of cold marrow extraction on long bone diaphysis (percussion marks and bone flakes) since grease rendering is rarely observed without previous marrow extraction (Outram, 2001). We could also expect to find concentrations of heat-cracked stones ethnographically used to heat water in a container made of wood or skin necessary to extract grease from crushed cancellous bones (Vehik, 1977; Binford, 1978; Manne, 2012), although this criterion is questionable since it has been demonstrated that it is possible to boil water in perishable containers without the use of heated stones (Costamagno and Rigaud, 2013; Speth, 2015).

The identification of bone grease exploitation from archaeological faunal assemblages can be very tricky because of the numerous taphonomic processes (carnivore action, and post deposition attrition) that can mimic the criteria normally used to identify anthropogenically induced bone fragmentation, such as the underrepresentation of long bone epiphyses in relation to shaft portions (Costamagno, 2013; Morin and Soulier, 2017). However, a suite of diagnostic criteria for grease exploitation was recently published by Morin and Soulier (2017) based on experimental archaeology, including morphological criteria such as the presence of crushing marks, tearing marks, and micro-inclusions from contact with hammerstones or anvils.

While grease rendering would mainly produce unburned fragmented bones, the use of bones for fuel results in burned bones associated with hearths. Experimental studies have demonstrated the utility of cancellous bone (particularly whole epiphyses) as complementary fuel to other combustibles such as wood (Théry-Parisot et al., 2004; Costamagno et al., 2005; Marquer et al., 2010; Morin, 2010). The intentional burning of bone elements for fuel would result in a highly fragmented faunal assemblage with a high proportion of cancellous burned bones. The use of bones for fuel in Paleolithic contexts could derive from two potential incentives. The bones were either burned for specific activities such as lighting, heating, drying, or other (ritual, elimination of animal waste), or they were burned for opportunistic purposes when faced with a lack of other

380 combustible (Marquer et al., 2010). However, bones do not have the same combustion
381 properties as wood. While the latter is good for fire maintenance, indirect cooking, and
382 transformation of raw material, bones do not produce embers and are therefore more
383 adapted to producing durable flames for lighting, heating, cooking, and drying (Théry-
384 Parisot et al., 2004).
385
386 When faced with a challenging taphonomic context such as the highly fragmented faunal
387 record at Riparo Bombrini, all three proxies for resource management are very difficult to
388 discuss. To partially remediate to this issue, we integrated the systematic ZooMS
389 sampling to our archaeozoological and taphonomic analyses. ZooMS collagen
390 fingerprinting takes advantage of the preservation properties of collagen which is the
391 most abundant protein in bone, present at more than 22% by dry weight of modern bone
392 (e.g. Buckley, 2018). The method is based on the observation that the triple-helix
393 structure of the collagen protein contains enough differences to be useful for taxonomic
394 separation (Buckley et al., 2009). ZooMS collagen fingerprinting has therefore proved to
395 be an excellent tool to identify a wide range of wild fauna (Buckley et al., 2010, 2014;
396 Buckley and Kansa, 2011) in order to improve NISP **s**tatistical significance. To a lesser
397 degree, it also helps improving the skeletal representation when sampling identifiable
398 skeletal parts of morphologically similar taxa (e.g. roe deer versus red deer) and of broad
399 categories (e.g. Ungulate size 2) (see Pothier Bouchard et al., 2019 for discussion). To
400 date, studies featuring the application of mass sampling (>100 bone samples) through
401 ZooMS collagen fingerprinting of Paleolithic faunal assemblages have mainly focused on
402 either identifying ancient hominin bone fragments (Brown et al., 2016; Devièse et al.,
403 2017; Welker, 2018), or proving the usefulness of the method as a complementary tool
404 for taxonomic identifications and assessing bone collagen preservation (Buckley and
405 Kansa, 2011; Welker et al., 2015, 2017; Buckley et al., 2017). While there have been
406 recent limited attempts at exploring the relationship between faunal composition and
407 bone fragmentation (Sinet-Mathiot et al., 2019), there remains much conceptual and
408 methodological work to be done in order to systematically integrate ZooMS into full
409 archaeozoological and taphonomic studies of Paleolithic faunal assemblages. With this
410 goal in mind, this study uses the Protoaurignacian faunal remains from the site of Riparo

Bombrini to provide what is, to our knowledge, the first attempt at such an integration of these three lines of evidence in order to yield new information about human behavioral adaptations, the sum of which is greater than its individual parts.

2 Material and Methods

The faunal assemblage in study was sampled from two Protoaurignacian levels (A1 and A2) on three areas of the site. These areas (south, north, and outside) have been selected to be representative of three different features of the site (Fig. 3). The south area was entirely excavated from 2015 to 2017 and contained a pit feature in both levels A1 and A2 (mainly concentrated on square FF3) which is interpreted as a discard feature. The north area was excavated between 2002-2005 and contains cuvette type hearth features in both levels (concentrated on square DD1). The outside area was mostly excavated in 2002 and corresponds to two squares located outside the rockshelter where levels A1 and A2 are more difficult to discriminate. This last area will therefore be attributed to a level A1-A2 in this study.

2.1 Archaeozoology

A total of 32,351 bone fragments were analysed. Taxonomic identifications were conducted using gross morphology and ZooMs. Skeletal remains that could not be identified to a species were assigned to a size category adapted from Brain (1981). The assemblages were quantified using standard archaeozoological methods (NISP, MNE, MNI; see Grayson, 1984; Lyman, 2008). When possible, age at death was determined using tooth wear stages on isolated teeth (Grant, 1982; Hillson, 2009) and epiphyseal fusion stages on long bones (Purdue, 1983; Zeder et al., 2015). The relative abundance of taxa is usually quantified using a combination of NISP and MNI in archaeozoology to account for the effects of fragmentation on MNI. However, the extensive fragmentation of the Riparo Bombrini assemblages considerably hinders effort to quantify MNI, since the MNI values for all of the identified taxa only yield one individual (or two in the cases where a juvenile element was identified). We will therefore only consider the NISP to evaluate the abundance of each taxon in the present study. Furthermore, the abundance of skeletal remains is usually measured using MNE, but this index is equally affected by the

state of fragmentation of the faunal assemblages. We therefore regrouped skeletal elements within skeletal portion categories (i.e. head, axial post-cranial, upper limb, lower limb, indeterminate limb, and foot; adapted from Stiner (2002b)) for each ungulate taxa to better allow interpreting carcass transportation strategies at Riparo Bombrini.

The limitations of NISP, MNI and MNE have been discussed elsewhere at length (Grayson, 1984; Marean et al., 2001; Lyman, 2008; Reitz and Wing, 2008; Cannon, 2013; Morin et al., 2016) and apply to our study, as demonstrated by the paucity of identifiable skeletal elements, which we attribute to the high degree of fragmentation. Unfortunately, MNE counts are used to calculate MAU (minimum anatomical unit) counts which are used in conjunction with indices of bone density to assess the impact of density mediated attrition on an assemblage, and in conjunction with indices of carcass utility, such as the FUI (food utility index, see Metcalfe and Jones, 1988) to evaluate carcass transportation strategies.

The extent of post-depositional attrition is generally evaluated by calculating the correlation coefficient of % survivorship values and their corresponding bone mineral density (%survivorship/BMD) (Lyman, 2008). The %survivorship values are calculated using MNE of a particular skeletal part in relation to the maximum MNE in the assemblage (Lyman, 2008). Because denser skeletal tissues are more able to resist post-depositional breakage over time (Lyman, 1994; Stiner, 2002b; Lam and Pearson, 2005; Costamagno, 2013; Morin and Soulier, 2017) density mediated attrition tends to result in the underrepresentation of long bone epiphyses, as well as the relative loss of smaller taxa and young animals (Lyman, 1994). However, given the low MNI counts in our assemblages we were unable to test the impact of post-depositional attrition on skeletal representation using conventional methods.

Finally, another limitation related to quantification in archaeozoology is the interdependence of faunal remains, described as the probability of counting a skeletal element or an individual animal multiple times. This problem is usually tackled by comparing NISP for each taxon with their associated MNI in order to evaluate the degree

of interdependence on the site and the likelihood of it influencing the NISP count. Using the MNI is not an option in this study, however, and we should therefore be aware that one animal can easily be counted more than once, which is especially true considering that we have analysed a number of bone shaft fragments with ZooMS. However, chances are that the interdependence is not randomly distributed at Bombrini given that we have sampled three zones with well-defined archaeological features. This gives us the opportunity to better predict potential faunal aggregates associated with the discarding pit or the hearth features, for example.

2.2 Taphonomy

As discussed earlier, discriminating between the different taphonomic processes responsible for post-depositional attrition is crucial in order to be in a position to discuss human behavior. For example, the underrepresentation of ungulate long bone epiphysis can be created by carnivore gnawing (Haynes, 1983; Blumenschine, 1988; Faith et al., 2007), anthropic grease exploitation (Vehik, 1977; Outram, 2001; Outram et al., 2005; Costamagno, 2013; Morin and Soulier, 2017), and the use of bone as fuel (Théry-Parisot et al., 2004; Costamagno et al., 2005; Morin, 2010).

We attempted to evaluate the differential preservation of cervids skeletal elements (cervids are the most abundant taxa in the faunal collection), we combined all identified skeletal elements of the taxon categories corresponding to "*Cervus"* and "cervid", we first calculated the skeletal part profile by calculating %MAU using this equation: ([MAU*i*]100)/(maximum MAU in the assemblage) where *i* is a particular skeletal element part such as "distal femur" or proximal humerus" (Lyman, 2008, p. 238). We then calculated the correlation coefficient between the resulting %MAU and BMD derived from Lam et al. (1999), which is equivalent to the %suvivorship/BMD. Finally, we analyzed the resulting data with the nonparametric Spearman's correlation (r_s), to calculate the correlation coefficient, where H_0 = there is no link between bone mineral density and skeletal element survivorship (%MAU). The nonparametric equivalent of

Pearson's correlation is also chosen here because of the very small sample size (N=9) and the fact that the data is not normally distributed.

However, the lack of MNE left us no choice but to find alternative ways to evaluate post-depositional bone attrition. We therefore had to turn on the indeterminate fraction of the faunal assemblage and to rely on the more generalized fact that denser skeletal tissue (mostly the cortical part of long bones) tends to better resist post-deposition attrition such as weather exposure, acidity of the surrounding sediments, water action, and carnivore action (Lyman, 1994) by comparing the proportion of bone type categories (cortical, cancellous, axial cancellous, and appendicular cancellous).

To collect a maximum of taxonomic information from the heavily fragmented assemblages, we analyzed the non-identifiable (or indeterminate) bones in an efficient and rapid way, each bulk bag of fragmented bones collected in the sieve was first sorted between six size classes according to their maximum length (0-20 mm, 20-30 mm, 30-40 mm, 40-50 mm, 50-60 mm, 60-80 mm, 80-100 mm, >100 mm). Within each size class, any identifiable element was set aside, and the rest of the bones was subdivided into color classes to first separate burning levels (burned 1: slightly burned, burned 2: carbonised, burned 3: calcined; adapted from (Stiner et al., 1995) and (Marques et al., 2018)) from unburned bones, and bone types (cortical, cancellous, and when possible, cortical from bone shafts, axial cancellous, and appendicular cancellous). Each subdivision was finally quantified and weighed with a Tangent KP-103 scale (Max 120.0g, d=0.1g). When bone cortical surfaces were preserved (very rarely within size class 0-20 mm), long bone shafts were analysed for fracture freshness (Villa and Mahieu, 1991; Outram, 2001) to calculate the mean Fracture Freshness Index (FFI; see Outram, 2001) within each archaeological level and taphonomic alterations including concretion, root and microorganism etching, manganese coloration, trampling, anthropic percussion marks, cut marks, and bone manufacture (Behrensmeyer, 1978; Lyman, 1994; Fisher Jr, 1995; Stiner et al., 1995). Plotted finds, identifiable bones (complete enough to be identified to the element), and teeth were also fully characterised with taphonomic alterations mentioned above. Surface modifications were analysed using a Dino-Lite Edge Digital Microscope 20X-220X enhanced DOF used with DinoCapture 2.0 software.

2.3 ZooMS Sampling Integrated to the Faunal Analyses

Because collagen preservation is very compromised at Riparo Bombrini, we applied a screening method developed and tested elsewhere (Pothier Bouchard et al., 2019) using an Agilent 4500a, portable FTIR instrument equipped with a single-bounce diamond ATR and internal battery, while conducting the faunal analysis described above in Genoa. We systematically selected 20 to 30 bone samples to screen for ZooMS in each stratigraphic unit of every square meter analysed. Plotted finds and morphologically identifiable bones (anatomical parts) were prioritised, and then a sample of smaller fractions (10-30 mm bone fragments) was randomly selected while trying to be representative of the diversity of bone types (cancellous, cortical, etc.) and animal size (diversity of cortical thicknesses based on size classes originally described by Brain, 1981). We also attempted to sample fetal and juvenile bone fragments when collagen was preserved. This was done to improve the statistical significance of the skeletal representation (by sampling morphologically identifiable parts of unknown species), the diversity of the faunal spectra (by sampling a diversity of cortical thicknesses), and the seasonality evidence (by sampling fetal and juvenile bones). This sampling strategy helped improving the resulting data but is also the subject to some limitations since collagen preservation often varies according to the same taphonomic effects that contribute to bone fragmentation (Stiner et al., 1995; Bar-Oz and Munro, 2004; Trueman et al., 2004; Dal Sasso et al., 2016; Le Meillour et al., 2018). In that sense, issues related to NISP and MNE measurements such as the interdependence of skeletal parts and the aggregation effect could be enhanced with ZooMS identification as discussed earlier (see Pothier Bouchard et al., 2019 for further discussion). Nevertheless, ZooMS identification greatly improved our data at Riparo Bombrini. When ZooMS identifications failed because of a lack of bone collagen, the data was collected to calculate a ZooMS success rate (successful ZooMS identification/failed ZooMS identification*100) which can in turn provide insights into faunal preservation in the different areas of the site.

Each selected bone was sampled for FTIR analysis. Approximately 1 mg of powder was produced using a mortar and pestle, and the powder was then pressed against the clean diamond crystal with an anvil and was discarded following measurement. Measurements

565 were taken with the automatic settings of the instrument with a spectral range from 4000-
566 650 cm^{-1}, at 4 cm^{-1} resolution, with 64 co-added scans. Each spectrum was exported in
567 the Grams spectral format (.spc), and processed using Resolutions Pro (Agilent) to
568 measure Amide I and Phosphate v3 peaks using measurement system N described in
569 (Pothier Bouchard et al., 2019). The results were then exported to Microsoft Excel for
570 calculation of the CO/P ratio. The screening threshold of 0.4 was selected; entailing a
571 sample was rejected when its CO/P ratio was less than 0.4. When the calculated CO/P
572 ratio scored 0.4 or more, it was considered suitable for ZooMS analysis.
573
574 Overall, a total of 612 bones were processed for acid-soluble ZooMS analysis following
575 the method adapted from Buckley et al. (2009). The use of this acid-soluble fraction
576 allows for potential future use of the insoluble pellet (obtained with the original bone
577 pellet that is air-dried and stored after ZooMS analysis) for isotopic analyses, whether
578 stable isotopes for dietary inferences (van der Sluis et al., 2014) or radiocarbon for dating
579 (e.g., Harvey et al., 2016). For each bone sample, approximately 25-50 mg of bone
580 powder was placed in a 1.5mL Eppendorf tube and demineralised with 1 mL of 0.6 M
581 hydrochloric acid (HCl) overnight (18 h, 4°C). Following the centrifugation at 12,400 × g
582 for 1 min to precipitate the pellet, 500 µL of the acid-soluble fractions were ultrafiltered
583 with 10 kDa molecular weight cut-off membranes (MWCO), centrifuging again at 12,400
584 × g for 30 min. The remaining 500 µL of HCL solution was saved as a back-up.
585 Following demineralisation, two independent volumes of 500 µL of 50 mM ammonium
586 bicarbonate (ABC) were added to the ultrafilter to wash the filter, centrifuging at 12,400
587 × g for 30 min and discarding the through-flow after each spin. The collagen was then
588 recovered with 200 µL 50 mM ABC. Half of the resulting ABC solution was saved as
589 back-up. The remaining 100 µL was put in a fresh Eppendorf tube and digested with
590 trypsin overnight (18h, 37°C). 1µL of the sample was spotted the next day on a Bruker
591 mass spectrometer (MS) target plate with 1µL of α-cyano-4-hydroxcinnamic acid matrix
592 solution to allow co-crystalisation and air dried following Buckley et al. (2016). MALDI-
593 MS analyses were carried out on a Bruker Ultraflex II instrument, with a *m/z* window of
594 700-3,700 mass units and up to 2,000 laser acquisitions per spot. The obtained collagen
595 fingerprints were analysed with mMass software (v5.5.0) and animal species were

identified using previously published collagen peptide markers from reference spectra following Buckley et al. (2009, 2017). (See Supplementary Table S1 for all peptide markers used in this analysis and Figure S1 for examples of collagen fingerprints of each identified species at Riparo Bombrini).

After identifying all resulting spectra, 33 acid-soluble samples were targeted to be further purified and fractioned using reverse phase chromatography with C18 solid phase extraction (SPE) pipette tips, following the manufacturer's protocol (Varian, UK). Each 100µL sample was first acidified with 10µL 0.1% trifluoroacetic acif (TFA) and eluted into two fractions of actenonitrile (ACN) concentrations: 10% ACN/0.1%TFA, and 50% ACN/0.1% TFA. Fractions were air-dried for 48 h and resuspended in 10µL 0.1%TFA. 1µL of each fraction was then spotted using the same procedure as the original acid-soluble samples. This method helped clarify some of our cervid identifications by improving the signal intensity of the A2T67(G) biomarker that is crucial to distinguish between *Cervus* (*m/z* value of 3033) and *Capreolus* (*m/z* value of 3059.4) (see Buckley et al. (2010) for further discussion on the isolation of collagen-peptid markers).

While certain deer genera can be discriminated with collagen fingerprinting, it should be noted that red deer (*Cervus elaphus*) and fallow deer (*Dama dama*.) are too closely related to be distinguished with ZooMS (Buckley and Kansa, 2011). Since anecdotal fallow deer specimens were identified at Bombrini in the past (Holt et al., 2019), it is therefore not impossible that some of our *Cervus* identification also includes *Dama* specimens. Fortunately, those species are generally associated with similar environmental conditions and have similar behaviors, so the impossibility of discriminating between them should not be a major problem for our interpretations.

3 Results

3.1 NISP and Skeletal Representation

The NISP results listed in Table 1 clearly show how the ZooMS provides a more complete picture of the Protoaurignacian faunal assemblages from Riparo Bombrini. Even with the combined ZooMS and morphological identification (Table 1, Fig. 4),

627 however, the identification rate is still very low (1.2%). A large portion of the identified
628 taxa corresponds to a broad "ungulate" category represented in yellow in Figure 4 (26%
629 of total NISP). Nevertheless, as also shown in Figure 4 we were able to characterize and
630 compare the taxonomic composition of level A1 (Total NISP: N=47) and level A2 (Total
631 NISP: N=51). We observe that cervids (mainly represented by red deer - *Cervus elaphus*,
632 but also roe deer - *Capreolus*) are the most abundant taxa in both levels. However, over
633 40% of the specimens in each level is represented by other ungulate taxa; bovines
634 (*Bos/Bison*) and caprids (*Capra)* are slightly more abundant in Level A1, as opposed to
635 Level A2 in which wild boar (*Sus*) and horse (*Equus*) are a little more abundant.
636
637 Figure 5 shows the skeletal representation of identified taxa from combined levels A1
638 and A2 comparing morphological identification and the ZooMS results. The diagrams
639 demonstrate how the ZooMS improved the skeletal representation data which was
640 otherwise mostly restricted to the identification of anatomical elements within the
641 "ungulate" category and the under-representation of most anatomical elements with the
642 exception of teeth for most taxa. They also reveal that skeletal elements from all
643 anatomical portions of ungulates, cervids and caprids (except the feet and upper limb for
644 caprids) are found on the site. On the other hand, bovines are only represented by axial
645 elements and a high number of bone shaft fragments (N=20), all identified with ZooMS.
646 Equids are represented by a few teeth, some easily morphologically identifiable bone
647 fragments from the lower limbs (tibia, carpal/tarsal), and a ZooMS identified femur.
648 Suids are only represented by five teeth and two phalanges. The spatial and stratigraphic
649 correspondence of the identified skeletal elements for these taxa are described in the
650 supplemental information (Table S2).
651
652 Figure 6 shows the relationship between %MAU of cervids (*Cervus* + "cervid") and bone
653 mineral density. Most of the skeletal parts are represented by a single skeletal element,
654 which resulted in a statistically insignificant correlation between %MAU and BMD (r_s =
655 -0.24, p = 0.56)

3.2 Sex, Age, and Seasonality

There are currently no reliable data that could strongly indicate a preferred season of occupation in the Riparo Bombrini Protoaurignacian faunal assemblages. Except for the bovines, most of the documented hunted taxa are not particularly migratory animals and could have been available around the site year-round. A few cervid antler fragments could indicate either the acquisition of male animals or the gathering of fallen antlers. Lastly, the very few age diagnostic skeletal elements listed in Table 2 show the presence of at least three juvenile taxa on the site and some fetal skeletal remains, unfortunately too fragmented to be identified to element or taxon. Interestingly enough, all bone fragments corresponding to juvenile taxa and fetal bones come from either level A1-A2 or level A2. This could suggest seasonal occupations, namely spring occupations, in level A2.

3.3 Fragmentation and Taphonomy

Figure 7 shows the distribution of all faunal remains within six fragment size classes. The fact that the first size category (0-20 mm) is the largest attests to the fact that the overall degree of fragmentation of the Protoaurignacian faunal remains is extremely severe. The logged data (LOG 10) in Figure 7 shows that the faunal remains are slightly more fragmented in the south area, and especially in Level A2: remains are more abundant in the 0-20 mm size category and proportionally less abundant than the rest of the collection in the larger size categories. On the other hand, the outside area of the site contains a higher proportion of larger bones (>30 mm) than the rest of the collection.

Table 3 summarises all taphonomic data recorded on long bone shaft fragments that helped further characterise the preservation state of the faunal remains and all anthropic traces found on bone surfaces. The mean FFI scores show a clear dominance of dry fractures throughout the collection. While some slight preservation variability can be observed between the site areas (the scores are slightly higher inside the rockshelter, than outside) when comparing mean FFI scores, it is not significant enough to assess the nature (anthropic or post-depositional) of this variability. The %ZooMS success, however, demonstrates a clear preservation bias. Indeed, 78% of the bone samples

recovered outside the shelter yielded enough well-preserved collagen to allow ZooMS animal identification. In contrast, ZooMS success was never greater than 30% inside the rockshelter. This indicates that some taphonomic effects played a greater role in collagen and bone diagenesis inside the rockshelter.

The main post-depositional alterations observable on long bone shaft surfaces, namely concretion, root etching, and manganese coloration, are presented in Figure 8. Carnivore gnawing is episodic on the faunal assemblage and only one wolf specimen was found in level A1 (Fig. 4). Root and microorganism etching as well as a light manganese coloration are present throughout the collection but are especially pronounced on the faunal remains recovered outside the rockshelter. Concretion heavily affected the whole collection but particularly in the north area and outside the rockshelter.

Figure 9 and 10 show examples of anthropic actions recovered in the Protoaurignacian faunal collection at Riparo Bombrini and listed in Table 2: a bone needle tip located in the south area (Fig. 9), a bone flake (or splinter) located outside the rockshelter (Fig. 9), a grooved bone located in the north area, and burned bones covered with dots of ochre concentrated near the hearth feature (Fig.10).

Figure 11 shows the proportions of six bone types (appendicular cancellous, axial cancellous, indeterminate cancellous, appendicular cortical or bone shaft, and indeterminate) in eight size classes (0-20 mm, 10-20 mm, 20-30 mm, 30-40 mm, 40-60mm, 60-80mm, 80-100mm, and 100<mm) within each levels and site areas. First, there is some spatial patterning in these data. Compared to the south and the outside areas, a larger proportion of cancellous bones (mostly indeterminate, but also axial and appendicular) are distributed in the north area, which is where hearths were found in both levels. In contrast, the south area, interpreted as having been used mainly as a trash pit in both levels, is dominated by indeterminate and bone shaft fragments, while a mixture of bone types can be found outside the rockshelter, including a slightly higher proportion of better preserved and bigger flat bones, mostly rib fragments. Second, comparing Levels

A1 and A2 inside the rockshelter, we can observe a higher proportion of cancellous bones in Level A2 both in the north and south areas.

Figure 12 shows the proportion of burned and unburned bone fragments distributed by bone type (appendicular cancellous, axial cancellous, indeterminate cancellous, appendicular cortical or bone shaft, and indeterminate) within each level and in each site area. Comparing the site areas, one striking observation is that outside the rockshelter, few bone shaft fragments or flat bones are burned. In contrast, over 70% of appendicular and indeterminate cancellous bones are burned. Less than 10% of axial cancellous bones are burned, however, thus displaying a different pattern from the other two types of cancellous bones. The indeterminate category, which is the most abundant, generally tends to follow the same pattern of fragmentation as the cortical bone as it mostly contains very small (>10mm) fragments with no intact surfaces. The same trends are observed in the south area inside the rockshelter, although with slightly higher proportions of burned bones across all bone type categories, except for appendicular cancellous bones. Finally, the hearth area (north) shows a distinct pattern, since it displays a much higher proportion of burned, cancellous bones. This pattern is especially pronounced for level A2 and it is coupled with a high concentration of calcined bones across all bone type categories. Calcined bones are generally associated with direct exposure of a bone surface with high temperatures such as those produced by flames. Also, the distinct pattern observed on axial cancellous bones outside the rockshelter is not apparent inside the rockshelter (Fig. 12).

Finally, figure 13 shows a summary of all anthropic subsistence-related data recovered on the site (NISP, skeletal representation, anthropic marks, etc.) spatially contextualized in two faunal distribution maps corresponding to level A1 and level A2.

4 Discussion

4.1 Faunal Diversity and Hunting Strategies

Before including the ZooMS identification results, the total NISP included only 16 fragments identified to species and a few bones identified to broader categories (cervid,

748 bovid, carnivore, and ungulate). Unfortunately, 409 of the 644 ZooMS samples were too
749 poor in collagen to provide taxonomic identification (Table 2). This issue will be
750 addressed in the future by tightening our screening threshold in the sampling process with
751 a portable FTIR. Nevertheless, the 235 positive ZooMS samples considerably improved
752 our understanding of the diversity of fauna hunted during the Protoaurignacian (Fig.4).
753 As expected, cervids, mainly red deer but also some ZooMS identified roe deer (N=2),
754 dominate the faunal assemblage in both levels. However, bovines, mountain goats,
755 horses, and wild boars also seem to have been regularly hunted, since they account for
756 more than 40% of the NISP (Fig. 4) in both levels. Even if our sample size remains very
757 low, the diversity of the faunal assemblage, which is comparable in level A1 and level
758 A2, points to more generalist, rather than specialised hunting strategies.
759
760 As concerns paleoenvironmental reconstructions, the macrofauna does not disagree with
761 previous reconstructions based on pollen and microfauna (Holt et al., 2019). Cervids in
762 both levels are compatible with forested environments. Equids in both levels as well and
763 one specimen of rhinoceros in level A1-A2 suggest the presence of an open plain close to
764 the site. However, the proportions of the different species do not specifically point
765 towards warmer conditions in Level A1. On the contrary, while proportions of caprids are
766 similar in both levels, the higher proportion of bovines and a lower proportion of wild
767 boar would indicate colder conditions and more open habitats. However, environmental
768 reconstructions based on the presence and absence of macrofauna can sometimes be
769 misleading as paleoenvironments are different from today and often contain a mosaic of
770 ecotypes and extinct taxa that are difficult to compare with extant environments (e.g.
771 hyenas living in the same ecotype as mammoths, reindeers, horses, etc.). Likewise, it is
772 important to appreciate that the faunal assemblages from both levels, while distinct,
773 nonetheless represent palimpsests accumulated over several millennia during a period of
774 remarkable climatic volatility, so that the presence of a few cold-adapted species is not
775 enough to reflect distinct environmental conditions. Furthermore, the specific species of
776 bovine at Riparo Bombrini is unknown and could lead to different environmental
777 reconstructions as it is well documented that some extant species of bison live in small
778 groups with local mobility in forested environments while others live in arid conditions

779 and migrate in large herds on open steppes (Julien et al., 2012). It should also be noted
780 that most of the bovines identified on the site comes from the exterior of the rockshelter
781 in which Levels A1 and A2 are undifferentiated (Fig. 13). Also, the bovines used to
782 compare levels A1 and A2 are very few and were almost all clustered within the eastern
783 section of the hearths (Fig. 13). This cluster could therefore be subject to archaeological
784 aggregate biases.
785
786 While our sample is small and too aggregated to resolve the question of environmental
787 patterns, we have already pointed out that the picture that emerges is one of overall
788 continuity in animal procurement strategies across Levels A1 and A2, which is especially
789 interesting from a behavioral perspective. The abundance of red deer in the region comes
790 with as no surprise and hunter-gatherers would have been able to take advantage of their
791 abundance around the site year round. However, the fact that bovines, wild goats, wild
792 boars, and horses were also part of the targeted species hints towards a generalist
793 strategy, which suggest Protoaurignacian foragers exploited the whole spectrum of
794 animals available locally.
795
796 One way to verify if Protoaurignacian hunter-gatherers were indeed hunting on a local
797 scale is to reconstruct carcass transport through the information available from skeletal
798 representation. Unfortunately, because the skeletal representation data are very scarce
799 (Fig. 5), very few interpretations can be securely drawn from them. Nevertheless, Figure
800 5 suggests that some cervid carcasses, represented by the presence of all body portions in
801 both Protoaurignacian levels, were brought to the site whole, implying that they were
802 available close to the site. The diversity of skeletal parts for the other animal species is
803 very poorly documented, but anecdotally, axial and appendicular elements are present for
804 most taxa, again suggesting the transport of at least a few whole carcasses, since axial
805 skeletal parts are often left at the kill site if the animals are hunted far from the base
806 camp. Similarly, both ungulate categories (size 2/3 and size 3/4) include skeletal remains
807 from most body portions. Another element supporting the idea that complete carcasses
808 were brought to Riparo Bombrini comes from the indeterminate fraction of the
809 assemblage. In fact, the constant presence of axial cancellous and flat bones (especially

outside the rockshelter) agrees with the hypothesis of a number of carcasses being brought back whole at Riparo Bombrini. In sum, despite the scarcity of the information provided by the relative abundance measurements and skeletal representation, the overall hunting strategy appears to have been a local generalist one throughout the Protoaurignacian.

4.2 Fragmentation, Bone as Food and More

Results from the taphonomic analysis indicate that most of the heavy bone fragmentation observed in the Protoaurignacian levels of Riparo Bombrini was caused by post-depositional forces, as suggested by the very high mean FFI scores in both levels which show a dominance of dry fractures (Table 2). Soil compaction, likely largely the result of blasting operations during the construction of the railway in the 19th century, coupled with concretion at least partially explains the heavy fragmentation and collagen degradation at the site (Fig. 8). Heavy concretion affects the entire collection inside the rockshelter, particularly in the north area, closer to the back wall of the rockshelter where the blasting events would have been most intense (Fig. 8). The concretion could also be related to taphonomic processes causing chemical bone dissolution (Weiner et al., 1995, 2007; Karkanas et al., 2000; Stiner et al., 2001; Trueman et al., 2004), but we would have to characterize sediment mineralogy in order to assess this (Stiner et al., 2001). This was unfortunately not possible at the moment.

However, some macroscopic observations agree with the fact that anthropic actions also contributed to bone fragmentation, and perhaps to some degree, also to bone diagenesis at the site. First, even though concretion particularly affected bone fragments from the north area, it is also present outside the rockshelter (in higher proportions than in the south area), coupled with heavy etching action, whereas the collagen is better preserved and the FFI mean score is lower in this area (Fig. 8, Table 2). This implies that different taphonomic processes occurred inside and outside the rockshelter. Second, while bone dissolution cannot be ruled out for the loss of smaller fragments in some areas at this point and should be assessed in the future since phosphate and carbonate diagenesis in bones is a known phenomenon in Mediterranean sites (Stiner et al., 2001), the diversity

841 of skeletal tissue documented at the site (Fig.12) indicates that more fragile bone (e.g.,
842 cancellous bones) is well represented inside the rockshelter and is in fact slightly less
843 abundant outside the rockshelter, where bone collagen is better preserved. If dissolution
844 events such as water flows had occurred inside the rockshelter during the
845 Protoaurignacian, the more fragile bones would have been the first to be destroyed. Given
846 these different patterns, it therefore seems warranted to propose that the heavy
847 fragmentation of bone remains in both Protoaurignacian levels at Bombrini is at least
848 partially due to human activities. This is further supported by the fact that underlying
849 Mousterian levels contain better preserved faunal remains (at least at the macroscopic
850 level). Additional factors support a high intensity of human occupation at the site
851 throughout the Protoaurignacian, namely the low incidence of carnivore modification
852 documented in both levels (Table 2, Fig. 8), the high density of archaeological remains,
853 and the preponderance of burned bones (Table 2, Fig. 12).
854
855 It is unsurprisingly very difficult to characterise carcass treatment on the site since, apart
856 from burned bones, evidence of anthropic actions is very scarce (Table 2) and is partially
857 masked by the high degree of dry fractures and bone surface erosion (?). Nevertheless, a
858 few cut marks, grooving marks, bone flakes, and bone tools were recovered from all parts
859 of the site (Table 2, Fig. 9). A small concentration of burned and unburned bones covered
860 with dots of red ochre was also uncovered in square DD1 in Level A2 (Fig. 10). Since the
861 ochre covers both fresh and dry bone fractures, this dotting is likely simply the result of
862 proximity of the bone fragments to numerous ochre fragments present in the sediment in
863 Level A2. Most of the fragments bearing percussion marks come from outside the
864 rockshelter, but a few are also found in the north area from Level A1 (Table 2, Fig. 13).
865 The bone flakes are spread across the three areas of the site and in both levels, but a
866 marked concentration is located in the north area from Level A2 (Table 2, Fig. 13). Cut
867 marks and bone tool manufacture marks (grooving) are very scarce and found in all parts
868 of the site. Finally, in both levels, all bone tools (awl and needle fragments) were
869 recovered in the southern part of the site (Table 2, Fig. 13).
870

As stated above, two kinds of human behaviors are known from the archaeological and the ethnographic records to produce heavily fragmented faunal assemblage: (1) bone marrow and grease extraction, and (2) the use of bones as fuel. Bone marrow extraction is a well-known behavior among prehistoric and extant high-latitude hunter-gatherer groups, among whom it is an almost universal behavior (Vehik, 1977; Binford, 1978; Outram, 2001). Considering the bone flakes and percussion marks on long bone shafts documented in both Protoaurignacian levels, it is reasonable to hypothesize that marrow extraction took place in Bombrini (Table 2). Furthermore, from a spatial perspective, two small bone flake concentrations can be seen. The first is located outside the rockshelter and is associated with a concentration of bones bearing percussion marks and a diversity of skeletal body parts including 11 unburned flat bone fragments (Fig. 13). These combined observations agree with the first stages of butchery and bone cracking away from the site's main living area. The second bone flake concentration is found in Level A2 and is located in the north area, close to the hearth. This second concentration is not associated with percussion marks on long bone shafts, either because they were not preserved or because those flakes are related to a different activity such as bone tool manufacture (Fig. 13). Diagnostic evidence of grease rendering is not detectable on the faunal remains at Riparo Bombrini. If at some point, there were concentrations of heavily crushed appendicular and cancellous bones bearing fresh fracture outlines on the site, they are now completely masked by post-depositional processes. In addition, no fire-cracked rocks have so far been recovered in the Protoaurignacian levels.

In contrast, diagnostic evidence of the use of bone as fuel is found in the high proportion of burned cancellous bones around the hearths (north area) compared to the other site areas. This is especially noticeable in Level A2, where cancellous burned bones represent 13.5% of the north area's assemblage compared to 6.0% in Level A1. However, in both levels, over 50% of bone fragments in the north area are burned (Fig. 12). Furthermore, in Level A2, a large proportion of the burned bones are in fact calcined (burned 3), especially within bone type categories corresponding to whole and fragmented epiphyses, flat bones, indeterminate cancellous, and axial cancellous bones. These patterns suggest that hunter-gatherers selected the spongy parts of the carcasses from both appendicular

and axial body parts filled with grease, to fuel the hearth to produce durable flames. This may have been done to perform specific illumination, heating, drying, rituals, and/or discard activities (Théry-Parisot et al., 2004; Costamagno et al., 2005; Marquer et al., 2010; Morin, 2010). Alternatively, the use of cancellous bone for fuel could have been related to the opportunistic use of spongy bones when faced with a lack of wood in the environment (potentially related to length of occupation).

4.3 Mobility and Resource Management at Riparo Bombrini

The data about subsistence patterns presented in this study also permit a refined understanding of what was so far known about mobility and resource management at Riparo Bombrini. Table 3 summarises the trends drawn from the available lithic, environmental and now faunal data and to compare them across Levels A1 and A2 to reach new insights about variability in Protoaurignacian behavior.

Previous studies had already highlighted continuity in some behavioral dimensions between the two levels, namely the dominance of bladelets produced within the same *chaîne opératoire* indicative of a flexible technocomplex (Riel-Salvatore and Negrino, 2018b, 2018a). The consistent production of very polyvalent hunting armatures throughout the Protoaurignacian is congruent with our conclusion that the faunal record indicates an overall generalist hunting strategy implemented close to the site. Along with the bladelet-based lithic technology that characterises the Bombrini Protoaurignacian, the hunting activities appear to have been flexible, allowing hunter-gatherers a great deal of resilience in the face of considerable environmental instability, including dramatic paleoclimatic shifts such as Heinrich Event 4 and the eruption of the Phlegrean Fields ca. 39ky cal BP. Thus, both hunting strategies and lithic technological organization combine to reinforce the interpretation of Bombrini having served as a base camp characterised by distinct, spatially discrete activity areas. Outside the rockshelter, the uniformly distributed faunal remains, the presence of percussion marks, cut marks, bone flakes, bone tool manufacture marks (grooving), and a diversity of skeletal body parts with mixed burned and unburned remains, are characteristic of different behaviors related to butchering activities, bone marrow extraction, and a general discard area (Fig.13). In

contrast, the north area is characterised by the presence of one cuvette-type hearth in each level, around which a more restricted set of activities was documented, including bone tool manufacture (grooving marks), the use of red ochre, and the use of bones as fuel, as suggested by the high concentrations of cancellous burned bones (Fig. 12). Finally, the south area contains a higher proportion of heavily fragmented burned and unburned faunal remains in addition to broken bone tools (awls and needles) concentrated in a depression interpretable as a refuse pit identified mostly in square FF3 (Fig.13).

In addition to this behavioral continuity in faunal exploitation, however, some notable differences also exist between the two levels, and these agree with the previous conclusions drawn from the lithic record. Indeed, variability in lithic technological organization has previously been interpreted to show that Level A1, which is associated with overall warmer climates, was characterised with a more residential mobility strategy while level A2 shows a logistical mobility strategy associated with colder climates and longer occupations of the base camp (Riel-Salvatore 2007, 2010). Several lines of evidence from Level A2 indicate that Protoaurignacian groups occupied the site for prolonged periods of time. First, faunal remains are more spatially concentrated inside the rockshelter, and more fragmented inside the discarding pit, which may indicate a greater degree of site maintenance. Second, the higher density of faunal remains in the north areas (A1: N=3756; A2: N=8283) in addition to a concentration of ochre and bone also indicate specific repetitive hearth-related activities over longer periods of time.

At first glance, patterns of carcass curation less clearly distinguish Levels A1 and A2, since both assemblages indicate the use of bones as fuel. Nevertheless, we propose that fuel management changed overtime, since in Level A2, all grease-rich skeletal parts of carcasses appear to have been systematically used as fuel, likely to extend flame durability. In Level A1, in contrast, the pattern appears to shift to a more sporadic use of cancellous bones as fuel. This scenario is strengthened by (1) the higher proportion of cancellous burned bones documented in Level A2 as a whole; (2) the higher proportion of calcined bones around the hearth in Level A2; and (3) by the fact that it also yielded an

overall much larger number of cancellous bones, including indeterminate, appendicular, and axial cancellous burned and unburned bones (A1: N=412; A2: N=1596).

Furthermore, the prolonged occupations in Level A2 are potentially associated with seasonal occupations of the site during spring and summer as demonstrated by the presence of fetal remains and a few juvenile ungulate taxa (Table 2). Seasonal occupations of the site are also congruent with a logistical mobility strategy.

5 Conclusion

In sum, this study has yielded important new methodological, empirical and behavioral insights into the Protoaurignacian occupations of Riparo Bombrini. These, in turn, have important implications for our understanding of some of the earliest *Homo sapiens* adaptations in Western Europe. Methodologically, the notion of *carcass curation*, as reconstructed by the crossing of archaeozoological, taphonomic, spatial and proteomic data, has been shown to have considerable analytical promise, in addition to providing a coherent framework to integrate interlocking sets of information gleaned from heavily fragmented faunal assemblages that can be seen as having only limited analytical potential from a traditional archaeozoological perspective. This approach further shows that a considerable amount of information can be extracted from challenging faunal assemblages, with distinct strands data combining to form more solid inferential cables that can serve as working hypotheses that can be integrated with other lines of evidence (e.g., lithics) and structure ongoing analyses at the site. Furthermore, the present paper is the first application of the ZooMS screening method first proposed elsewhere (i.e., Pothier Bouchard et al., 2019) to obtain usable data about prehistoric forager behaviors at Riparo Bombrini that complements and considerably enhances our understanding of prey selection by Protoaurignacian hunters.

This ties into the empirical contribution of this analysis, since our results provide the first detailed analysis of Protoaurignacian large mammal exploitation at the Balzi Rossi and indeed in the Liguro-Provençal arc more broadly. Historically, large fauna has been largely excluded from consideration in synthetic analyses of the Riparo Mochi sequence

994 (e.g., Kuhn and Stiner, 1998), outside of oblique mentions to its heavily fragmented state
995 (Tejero and Grimaldi, 2015, p. 68; Moussous, pers. comm.), which contrast to the
996 relatively better-preserved nature of the Gravettian faunal assemblages at the same site
997 (Tagliacozzo et al., 2012). This has led to a great deal of attention being paid to its
998 mollusk assemblage (e.g., Stiner, 1999) to the exclusion of the rest of the faunal
999 assemblage. Likewise, outside of a partial species list (Onoratini and Simon, 2004;
1000 Brugal et al., 2017), little is known about Protoaurignacian faunal exploitation patterns at
1001 nearby Grotte de l'Observatoire in Monaco, and a recent publication on the 2002-2005
1002 excavations at Riparo Bombrini is limited to species identification (Holt et al.,
1003 2019).Thus, our systematic application of the ZooMS proved to be an excellent means of
1004 tackling heavily fragmented faunal assemblages. Mass sampling with ZooMS
1005 fingerprinting does not solve all issues related to bone fragmentation in Paleolithic
1006 archaeozoology, however. As we have detailed elsewhere (Pothier Bouchard et al., 2019),
1007 much work remains to be done to develop an adequate conceptual framework to fully
1008 integrate ZooMS into archaeozoological research. Such a framework will need to eschew
1009 randomly sampling of hundreds of bones within the smaller indeterminate fraction of
1010 faunal assemblages in favor of tailoring sampling strategies to specific hypothesis-testing
1011 approaches that seek to answer questions related to past subsistence behaviors.
1012
1013 The present study is a first step in this direction, and our results show the promise of such
1014 efforts, since it has already yielded important new data about Protoaurignacian settlement
1015 dynamics at Riparo Bombrini, namely that animal carcasses, and especially those of red
1016 and roe deer, were in all likelihood brought whole to the site. Similarly, the evidence we
1017 present for systematic, large-scale marrow extraction is the first such evidence for these
1018 behaviors in *Homo sapiens* in the region and indicates a sustained effort at maximizing
1019 the nutritional utility of hunted prey. Additionally, the use of bones as fuel documented at
1020 Riparo Bombrini also broadens our understanding of carcass curation behaviors by
1021 human foragers, likely also suggesting a polyvalent use of fuel sources to sustain
1022 different kinds of flame and heat in different contexts. Finally, the combined impacts of
1023 purposeful fragmentation for marrow extraction and of the use of bone as fuel inside the
1024 rockshelter helps explain the heavily fragmented and initially challenging nature of the

faunal assemblages at Riparo Bombrini. It also highlights that modern taphonomic effects such as the impact of soil compaction resulting from railroad construction and demolition on the state of the faunal collection does not fully explain the state of the collections. This leads to the further implication that Protoaurignacian anthropic manipulations likely bear a substantial portion of the blame for the poor state of collagen preservation of the faunal remains recovered from inside the shelter. This is compounded by our demonstration that the Riparo Bombrini faunal assemblages yield extremely limited traces of carnivore modifications.

On the behavioral front, the results presented here also both support and nuance previous interpretations about the internal variability of the Protoaurignacian at Riparo Bombrini. First, it reinforces the idea that the technocomplex was an adaptable strategy that allowed a great deal of flexibility to respond to shifts in local conditions to favor the long-term resilience of the human occupation of the region. Specifically, the generalist strategy we evidenced in both Protoaurignacian levels at Bombrini indicates a broad, rather than narrowly focused subsistence strategy. This agrees well with the mollusk data from Riparo Mochi that suggest that foragers were broadening their diets from the very beginning of the Upper Paleolithic (Kuhn and Stiner, 1998; Stiner, 1999), another element that argues against a specialised subsistence base in the Ligurian Protoaurignacian. In both levels, it seems clear that the site was used as a base camp around which other activities on the landscape were organized.

That said, the faunal data from Level A2 also indicate that, during the accumulation of this level, the site was used for longer periods of time, as shown by the more organised spatial separation of activity areas and by the greater abundance of faunal remains that accumulated over the same site surface in that level compared to Level A1. To this we can add the apparent systematic use of cancellous bone to feed fires in Level A2 which contrasts with its more sporadic use for this purpose in Level A1. This again, may reflect longer occupation in Level A2 which, along with seasonal occupations of the site, agrees with previous interpretation of that level's lithic assemblage showing a more logistical land-use strategy, when the site would have been used as a base camp for prolonged

periods of time during a generally colder phase (Riel-Salvatore & Negrino 2018a, 2018b). In sum, the faunal data appear to dovetail nicely with what could be gleaned from the lithic record to underscore that the Protoaurignacian comprised a fair amount of internal variability, which is likely linked to its longevity as a human adaptive system in the region.

Finally, the faunal data presented in this analysis provide additional support for the adaptive polyvalence of the Protoaurignacian, showing it was able to weather very different climatic regimes. This therefore reinforces the previous conclusions of some of the authors that there is not, at least in the Ligurian region, a solid basis to argue that the Protoaurignacian was narrowly adapted to limited ecological conditions. This provides another explanation for the apparent longevity of the technocomplex as the quintessential early *Homo sapiens* adaptation in the region, in contrast to what other scholars have argued for other regions (Banks et al., 2013). While this does not resolve outstanding questions about the potential links, or lack thereof, between the Protoaurignacian and Early Aurignacian, the fact that an independent line of evidence, in this case animal bone assemblages, again supports the internal dynamism of the Protoaurignacian at the Balzi Rossi certainly highlights that such a reductive view of early modern human settlement dynamics is unwarranted at a continental scale. Further, the method employed here to approach the notion of carcass curation through the combination of archaeozoology, taphonomy and ZooMS and to link it to broader questions about land-use and settlement organization, shows that it holds much promise to extract meaningful behavioral data from even the most fragmented of assemblages. This opens a pathway to the study of comparable assemblages, such as those from nearby Riparo Mochi, for instance, in order to contribute to the necessary integration of technological and subsistence data to reach an appropriately complete view of the Protoaurignacian as an anthropological phenomenon (Soulier, 2013, 2014).

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7 Bibliography

Alhaique, F., Bisconti, M., Castiglioni, E., Cilli, C., Fasani, L., Giacobini, G., Grifoni, R., Guerreschi, A., Iacopini, A., Malerba, G., Peretto, C., Recchi, A., Ris, A.R., Ronchitelli, A., Rottoli, M., ThunHohenstein, U., Tozz, C., Visentini, P., Wilkens, B., 2004. Animal Resources and Subsistence Strategies. Collegium antropologicum. 28, 23–40.

Anderson, L., Bon, F., Bordes, J.-G., Pasquini, A., Teyssandier, N., 2015. Relier des espaces, construire de nouveaux réseaux : aux origines du Protoaurignacien et des débuts du Paléolithique supérieur en Europe occidentale. In: XXXVe Rencontres Internationales d'archéologie et d'histoire d'Antibes, Éditions APDCA. Presented at the Les systèmes de mobilité de la Préhisoire au Moyen Âge, N. Naudinot, L. Meignen, D. Binder, G. Querré, Antibes.

Andrefsky, W., 2009. The Analysis of Stone Tool Procurement, Production, and Maintenance. Journal of Archaeological Research. 17, 65–103.

Arobba, D., Caramiello, R., 2009. Analisi paleobotanica sui sedimenti del riparo Bombrini (Balzi Rossi, Ventimiglia). Bull. Musée Anthropologie Préhistorique Monaco. 49, 41–48.

Banks, W.E., d'Errico, F., Zilhão, J., 2013. Revisiting the chronology of the Proto-Aurignacian and the Early Aurignacian in Europe: A reply to Higham et al.'s comments on. Journal of human evolution. 30, 1e8.

Bar-Oz, G., Munro, N.D., 2004. Beyond cautionary tales: a multivariate taphonomic approach for resolving equifinality in zooarchaeological studies. Journal of Taphonomy. 2, 201–220.

Barshay-Szmidt, C., Normand, C., Flas, D., Soulier, M.-C., 2018. Radiocarbon dating the Aurignacian sequence at Isturitz (France): Implications for the timing and development of the Protoaurignacian and Early Aurignacian in western Europe. Journal of Archaeological Science: Reports. 17, 809–838.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology. 4, 150–162.

Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S.E., Sawyer, S., Panetta, D., Vicino, G., Starnini, E., Mannino, M.A., Salvadori, P.A., Meyer, M., Pääbo, S., Hublin, J.-J., 2015. The makers of the Protoaurignacian and implications for Neandertal extinction. Science. 348, 793–796.

1133 Berto, C., Santaniello, F., Grimaldi, S., 2019. Palaeoenvironment and palaeoclimate in
1134 the western Liguria region (northwestern Italy) during the Last Glacial. The small
1135 mammal sequence of Riparo Mochi (Balzi Rossi, Ventimiglia). Comptes Rendus
1136 Palevol. 18, 13–23.
1137 Bertola, S., Broglio, A., Cristiani, E., De Stefani, M., Gurioli, F., Negrino, F., Romandini,
1138 M., Vanhaeren, M., 2013. La diffusione del primo Aurignaziano a sud dell'Arco
1139 alpino. Preistoria Alpina. 47, 17–30.
1140 Binford, L.R., 1978. Nunamiut ethnoarchaeology. Academic Press, New York.
1141 Binford, L.R., 1980. Willow Smoke and Dogs' Tails: Hunter-Gatherer Settlement
1142 Systems and Archaeological Site Formation. American Antiquity. 45, 4–20.
1143 Blumenschine, R.J., 1988. An experimental model of the timing of hominid and
1144 carnivore influence on archaeological bone assemblages. Journal of
1145 Archaeological Science. 15, 483–502.
1146 Brain, C.K., 1981. The hunters or the hunted?: an introduction to African cave
1147 taphonomy. University of Chicago Press, Chicago.
1148 Brown, S., Higham, T., Slon, V., Pääbo, S., Meyer, M., Douka, K., Brock, F., Comeskey,
1149 D., Procopio, N., Shunkov, M., Derevianko, A., Buckley, M., 2016. Identification
1150 of a new hominin bone from Denisova Cave, Siberia using collagen fingerprinting
1151 and mitochondrial DNA analysis. Scientific Reports. 6.
1152 Brugal, J.P., 1999. Middle Paleolithic subsistence on large Bovids: La Borde and
1153 Coudoulous I (Lot, France). The Role of Early Humans in the Accumulation of
1154 European Lower and Middle Palaeolithic Bone Assemblages. Monographien des
1155 Römisch-Germanischen Zentralmuseums. 42, 263–266.
1156 Brugal, J.-P., Fourvel, J.-B., Fosse, P., 2017. Premières observations sur les guildes de
1157 carnivores de la grotte de l'Observatoire. Bulletin du Musée d'Anthropologie
1158 Préhistorique de Monaco. 47–60.
1159 Buckley, M., 2018. Zooarchaeology by Mass Spectrometry (ZooMS) Collagen
1160 Fingerprinting for the Species Identification of Archaeological Bone Fragments.
1161 In: Giovas, C.M., LeFebvre, M.J. (Eds.), Zooarchaeology in Practice: Case
1162 Studies in Methodology and Interpretation in Archaeofaunal Analysis. Springer
1163 International Publishing, Cham, pp. 227–247.
1164 Buckley, M., Collins, M., Thomas-Oates, J., Wilson, J.C., 2009. Species identification by
1165 analysis of bone collagen using matrix-assisted laser desorption/ionisation time-
1166 of-flight mass spectrometry. Rapid communications in mass spectrometry. 23,
1167 3843–3854.
1168 Buckley, M., Fraser, S., Herman, J., Melton, N.D., Mulville, J., Pálsdóttir, A.H., 2014.
1169 Species identification of archaeological marine mammals using collagen
1170 fingerprinting. Journal of Archaeological Science. 41, 631–641.
1171 Buckley, M., Gu, M., Shameer, S., Patel, S., Chamberlain, A.T., 2016. High-throughput
1172 collagen fingerprinting of intact microfaunal remains; a low-cost method for
1173 distinguishing between murine rodent bones. Rapid Communications in Mass
1174 Spectrometry. 30, 805–812.
1175 Buckley, M., Harvey, V.L., Chamberlain, A.T., 2017. Species identification and decay
1176 assessment of Late Pleistocene fragmentary vertebrate remains from Pin Hole
1177 Cave (Creswell Crags, UK) using collagen fingerprinting. Boreas. 46, 402–411.

1178 Buckley, M., Kansa, S.W., 2011. Collagen fingerprinting of archaeological bone and
1179 teeth remains from Domuztepe, South Eastern Turkey. Archaeological and
1180 Anthropological Sciences. 3, 271–280.
1181 Buckley, M., Whitcher Kansa, S., Howard, S., Campbell, S., Thomas-Oates, J., Collins,
1182 M., 2010. Distinguishing between archaeological sheep and goat bones using a
1183 single collagen peptide. Journal of Archaeological Science. 37, 13–20.
1184 Burke, A., 2006a. Neanderthal settlement patterns in Crimea: A landscape approach.
1185 Journal of Anthropological Archaeology, Multidisciplinary Approaches to the
1186 Study of Site Function and Settlement Dynamics in Prehistory. 25, 510–523.
1187 Burke, A., 2006b. Palaeoethology as an archaeological tool: a model for the social and
1188 spatial behaviour of E. hydruntinus. Equids in Time and Space. Oxbow Books,
1189 Oxford. 62–69.
1190 Cannon, M.D., 2013. NISP, Bone Fragmentation, and the Measurement of Taxonomic
1191 Abundance. Journal of Archaeological Method and Theory. 20, 397–419.
1192 Cardini, L., 1938. Recenti scavi dell'Istituto italiano di paleontologia umana alla Barma
1193 Grande di Grimaldi. Archivio per l'Antropologia e la Etnologia. 68, 385–389.
1194 Clark, G.A., Riel-Salvatore, J., 2006. Observations on systematics in Paleolithic
1195 archaeology. In: Transitions before the Transition. Springer, pp. 29–56.
1196 Clark, G.A., Riel-Salvatore, J., 2009. What's in a name? Observations on the
1197 compositional integrity of the Aurignacian. In: Camps, M., Szmidt, C.C. (Eds.),
1198 The Mediterranean from 50.000 to 25.000 BP: Turning Points and New
1199 Directions. Oxbow Books, Oxford, pp. 323–338.
1200 Costamagno, S., 2013. Bone Grease Rendering in Mousterian Contexts: The Case of
1201 Noisetier Cave (Fréchet-Aure, Hautes-Pyrénées, France). In: Clark, J.L., Speth,
1202 J.D. (Eds.), Zooarchaeology and Modern Human Origins: Human Hunting
1203 Behavior during the Later Pleistocene, Vertebrate Paleobiology and
1204 Paleoanthropology. Springer Netherlands, Dordrecht, pp. 209–225.
1205 Costamagno, S., Liliane, M., Cédric, B., Bernard, V., Bruno, M., 2006. Les Pradelles
1206 (Marillac-le-Franc, France): A mousterian reindeer hunting camp? Journal of
1207 Anthropological Archaeology, Multidisciplinary Approaches to the Study of Site
1208 Function and Settlement Dynamics in Prehistory. 25, 466–484.
1209 Costamagno, S., Rigaud, J.-P., 2013. L'exploitation de la graisse au Paléolithique.
1210 Presented at the 138e Congrès national des sociétés historiques et scientifiques,
1211 hal-01891712, Rennes, France, pp. 134–152.
1212 Costamagno, S., Théry-Parisot, I., Brugal, J.-P., Guibert, R., 2005. Taphonomic
1213 consequences of the use of bones as fuel. Experimental data and archaeological
1214 applications. In: Biosphere to Lithosphere, Proceedings of the 9th Conference of
1215 the International Council of Archaeozoology. Oxbow Books, Oxford. pp. 51–62.
1216 Dal Sasso, G., Lebon, M., Angelini, I., Maritan, L., Usai, D., Artioli, G., 2016. Bone
1217 diagenesis variability among multiple burial phases at Al Khiday (Sudan)
1218 investigated by ATR-FTIR spectroscopy. Palaeogeography, Palaeoclimatology,
1219 Palaeoecology. 463, 168–179.
1220 Delagnes, A., Rendu, W., 2011. Shifts in Neandertal mobility, technology and
1221 subsistence strategies in western France. Journal of Archaeological Science. 38,
1222 1771–1783.

1223 Demidenko, Y., Noiret, P., 2012. The Siuren I Aurignacian of Krems-Dufour type
1224 industries in the context of the European Aurignacian. Siuren I Rock-Shelter.
1225 From Late Middle Paleolithic and Early Upper Paleolithic to Epi-Paleolithic in
1226 Crimea. 343–357.
1227 Demidenko, Y.E., Otte, M., 2000. Siuren-I (Crimea) in the context of a European
1228 Aurignacian. Préhistoire européenne. 16, 133–146.
1229 Devièse, T., Karavanić, I., Comeskey, D., Kubiak, C., Korlević, P., Hajdinjak, M.,
1230 Radović, S., Procopio, N., Buckley, M., Pääbo, S., 2017. Direct dating of
1231 Neanderthal remains from the site of Vindija Cave and implications for the
1232 Middle to Upper Paleolithic transition. Proceedings of the National Academy of
1233 Sciences. 114, 10606–10611.
1234 Dinnis, R., Bessudnov, A., Reynolds, N., Devièse, T., Pate, A., Sablin, M., Sinitsyn, A.,
1235 Higham, T., 2019. New data for the Early Upper Paleolithic of Kostenki (Russia).
1236 Journal of Human Evolution. 127, 21–40.
1237 Domínguez-Rodrigo, M., Yravedra, J., 2009. Why are cut mark frequencies in
1238 archaeofaunal assemblages so variable? A multivariate analysis. Journal of
1239 Archaeological Science. 36, 884–894.
1240 Douka, K., Grimaldi, S., Boschian, G., del Lucchese, A., Higham, T.F., 2012. A new
1241 chronostratigraphic framework for the Upper Palaeolithic of Riparo Mochi (Italy).
1242 Journal of Human Evolution. 62, 286–299.
1243 Faith, J.T., Gordon, A.D., 2007. Skeletal element abundances in archaeofaunal
1244 assemblages: economic utility, sample size, and assessment of carcass transport
1245 strategies. Journal of Archaeological Science. 34, 872e882.
1246 Faith, J.T., Marean, C.W., Behrensmeyer, A.K., 2007. Carnivore competition, bone
1247 destruction, and bone density. Journal of Archaeological Science. 34, 2025–2034.
1248 Falcucci, A., Conard, N.J., Peresani, M., 2017. A critical assessment of the
1249 Protoaurignacian lithic technology at Fumane Cave and its implications for the
1250 definition of the earliest Aurignacian. PLOS ONE. 12, e0189241.
1251 Falcucci, A., Peresani, M., Roussel, M., Normand, C., Soressi, M., 2018. What's the
1252 point? Retouched bladelet variability in the Protoaurignacian. Results from
1253 Fumane, Isturitz, and Les Cottés. Archaeological and Anthropological Sciences.
1254 10, 539–554.
1255 Fisher Jr, J.W., 1995. Bone surface modifications in zooarchaeology. Journal of
1256 Archaeological method and theory. 2, 7–68.
1257 Gaudzinski, S., 2006. Monospecific or Species-Dominated Faunal Assemblages During
1258 the Middle Paleolithic in Europe. In: Hovers, E., Kuhn, S.L. (Eds.), Transitions
1259 Before the Transition, Interdisciplinary Contributions To Archaeology. Springer
1260 US, pp. 137–147.
1261 Gaudzinski, S., Roebroeks, W., 2000. Adults only. Reindeer hunting at the Middle
1262 Palaeolithic site Salzgitter Lebenstedt, Northern Germany. Journal of Human
1263 Evolution. 38, 497–521.
1264 Giaccio, B., Hajdas, I., Isaia, R., Deino, A., Nomade, S., 2017. High-precision 14 C and
1265 40 Ar/39 Ar dating of the Campanian Ignimbrite (Y-5) reconciles the time-scales
1266 of climatic-cultural processes at 40 ka. Scientific reports. 7, 45940.
1267 Grant, A., 1982. The use of tooth wear as a guide to the age of domestic ungulates.
1268 Ageing and sexing animal bones from archaeological sites. 109, 91–108.

1269 Grayson, D.K., 1984. Quantitative zooarchaeology: topics in the analysis of
1270 archaeological faunas. Academic Press, Orlando.
1271 Grayson, D.K., 1989. Bone transport, bone destruction, and reverse utility curves. Journal
1272 of Archaeological Science. 16, 643–652.
1273 Grayson, D.K., Delpech, F., 1998. Changing Diet Breadth in the Early Upper Palaeolithic
1274 of Southwestern France. Journal of Archaeological Science. 25, 1119–1129.
1275 Grayson, D.K., Delpech, F., 2002. Specialized Early Upper Palaeolithic Hunters in
1276 Southwestern France? Journal of Archaeological Science. 29, 1439–1449.
1277 Grimaldi, S., Porraz, G., Santaniello, F., 2014. Raw material procurement and land use in
1278 the northern Mediterranean Arc: insight from the first Proto-Aurignacian of
1279 Riparo Mochi (Balzi Rossi, Italy). Quartär. 61, 113–127.
1280 Guy Straus, L., 2005. A mosaic of change: the Middle–Upper Paleolithic transition as
1281 viewed from New Mexico and Iberia. Quaternary International, Armageddon or
1282 entente? The demise of the European Neandertals in Isotope Stage 3. 137, 47–67.
1283 Harvey, V.L., Egerton, V.M., Chamberlain, A.T., Manning, P.L., Buckley, M., 2016.
1284 Collagen Fingerprinting: A New Screening Technique for Radiocarbon Dating
1285 Ancient Bone. PLOS ONE. 11, e0150650.
1286 Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for
1287 gnaw damage to herbivore limb bones. Paleobiology. 9, 164–172.
1288 Higham, T., Douka, K., Wood, R., Ramsey, C.B., Brock, F., Basell, L., Camps, M.,
1289 Arrizabalaga, A., Baena, J., Barroso-Ruíz, C., Bergman, C., Boitard, C., Boscato,
1290 P., Caparrós, M., Conard, N.J., Draily, C., Froment, A., Galván, B., Gambassini,
1291 P., Garcia-Moreno, A., Grimaldi, S., Haesaerts, P., Holt, B., Iriarte-Chiapusso,
1292 M.-J., Jelinek, A., Jordá Pardo, J.F., Maíllo-Fernández, J.-M., Marom, A., Maroto,
1293 J., Menéndez, M., Metz, L., Morin, E., Moroni, A., Negrino, F., Panagopoulou,
1294 E., Peresani, M., Pirson, S., de la Rasilla, M., Riel-Salvatore, J., Ronchitelli, A.,
1295 Santamaria, D., Semal, P., Slimak, L., Soler, J., Soler, N., Villaluenga, A.,
1296 Pinhasi, R., Jacobi, R., 2014. The timing and spatiotemporal patterning of
1297 Neanderthal disappearance. Nature. 512, 306–309.
1298 Hillson, S., 2009. Teeth, Second Edition. ed, Manuals in Archaeology. Cambridge Univ.
1299 Press, Cambridge.
1300 Holt, B., Negrino, F., Riel-Salvatore, J., Formicola, V., Arellano, A., Arobba, D.,
1301 Boschian, G., Churchill, S.E., Cristiani, E., Di Canzio, E., Vicino, G., 2019. The
1302 Middle-Upper Paleolithic transition in Northwest Italy: new evidence from Riparo
1303 Bombrini (Balzi Rossi, Liguria, Italy). Quaternary International.
1304 Kadowaki, S., Omori, T., Nishiaki, Y., 2015. Variability in Early Ahmarian lithic
1305 technology and its implications for the model of a Levantine origin of the
1306 Protoaurignacian. Journal of Human Evolution. 82, 67–87.
1307 Karkanas, P., Bar-Yosef, O., Goldberg, P., Weiner, S., 2000. Diagenesis in Prehistoric
1308 Caves: the Use of Minerals that Form In Situ to Assess the Completeness of the
1309 Archaeological Record. Journal of Archaeological Science. 27, 915–929.
1310 Kelly, R.L., 1995. The foraging spectrum: diversity in hunter-gatherer lifeways.
1311 Smithsonian Institution Press, Washington.
1312 Kuhn, S.L., Stiner, M.C., 1998. Reports The Earliest Aurignacian of Riparo Mochi
1313 (Liguria, Italy). Current Anthropology. 39, S175–S189.

Lam, Y.M., Chen, X., Pearson, O.M., 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. American Antiquity. 64, 343–362.

Lam, Y.M., Pearson, O.M., 2005. Bone density studies and the interpretation of the faunal record. Evolutionary Anthropology: Issues, News, and Reviews. 14, 99–108.

Le Meillour, L., Zazzo, A., Lesur, J., Cersoy, S., Marie, A., Lebon, M., Pleurdeau, D., Zirah, S., 2018. Identification of degraded bone and tooth splinters from arid environments using palaeoproteomics. Palaeogeography, Palaeoclimatology, Palaeoecology. 511, 472–482.

Lugli, F., Cipriani, A., Capecchi, G., Ricci, S., Boschin, F., Boscato, P., Iacumin, P., Badino, F., Mannino, M.A., Talamo, S., Richards, M.P., Benazzi, S., Ronchitelli, A., 2019. Strontium and stable isotope evidence of human mobility strategies across the Last Glacial Maximum in southern Italy. Nature Ecology & Evolution. 3, 905–911.

Lupo, K.D., 2001. Archaeological skeletal part profiles and differential transport: an ethnoarchaeological example from Hadza bone assemblages. Journal of Anthropological Archaeology. 20, 361–378.

Lyman, R.L., 1985. Bone frequencies: differential transport, in situ destruction, and the MGUI. Journal of Archaeological Science. 12, 221–236.

Lyman, R.L., 1994. Vertebrate taphonomy. Cambridge University Press, Cambridge [England]; New York.

Lyman, R.L., 2008. Quantitative paleozoology. Cambridge University Press, Cambridge; New York.

Maíllo-Fernández, J.M., de Quirós, F.B., 2010. L'Aurignacien archaïque de la grotte El Castillo (Espagne) : caractérisation technologique et typologique. L'Anthropologie, Paléolithique supérieur. 114, 1–25.

Manne, T., 2012. Vale Boi: 10,000 years of Upper Paleolithic bone boiling. In: The Menial Art of Cooking: Archaeological Studies of Cooking and Food Preparation. Boulder: University Press of Colorado. Univesity Press of Colorado, pp. 173–199.

Marean, C.W., Abe, Y., Nilssen, P.J., Stone, E.C., 2001. Estimating the Minimum Number of Skeletal Elements (MNE) in Zooarchaeology: A Review and a New Image-Analysis GIS Approach. American Antiquity. 66, 333–348.

Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. Journal of Taphonomy. 1, 15–42.

Marquer, L., Otto, T., Nespoulet, R., Chiotti, L., 2010. A new approach to study the fuel used in hearths by hunter-gatherers at the Upper Palaeolithic site of Abri Pataud (Dordogne, France). Journal of Archaeological Science. 37, 2735–2746.

Marques, M.P.M., Mamede, A.P., Vassalo, A.R., Makhoul, C., Cunha, E., Gonçalves, D., Parker, S.F., Batista de Carvalho, L.A.E., 2018. Heat-induced Bone Diagenesis Probed by Vibrational Spectroscopy. Scientific Reports. 8, 15935.

Mellars, P., 2006. Archeology and the dispersal of modern humans in Europe: Deconstructing the "Aurignacian." Evolutionary Anthropology: Issues, News, and Reviews. 15, 167–182.

Mellars, P.A., 2004. Reindeer specialization in the early Upper Palaeolithic: the evidence from south west France. Journal of Archaeological Science. 31, 613–617.
Metcalfe, D., Jones, K.T., 1988. A reconsideration of animal body-part utility indices. American Antiquity. 486–504.
Moncel, M.-H., Fernandes, P., Willmes, M., James, H., Grün, R., 2019. Rocks, teeth, and tools: New insights into early Neanderthal mobility strategies in South-Eastern France from lithic reconstructions and strontium isotope analysis. PLOS ONE. 14, e0214925.
Morin, E., 2007. Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. Journal of Archaeological Science. 34, 69–82.
Morin, E., 2010. Taphonomic implications of the use of bone as fuel. Palethnologie. 2, 209–217.
Morin, E., Meier, J., Guennouni, K.E., Moigne, A.-M., Lebreton, L., Rusch, L., Valensi, P., Conolly, J., Cochard, D., 2019. New evidence of broader diets for archaic Homo populations in the northwestern Mediterranean. Science Advances. 5, eaav9106.
Morin, E., Ready, E., Boileau, A., Beauval, C., Coumont, M.-P., 2016. Problems of Identification and Quantification in Archaeozoological Analysis, Part I: Insights from a Blind Test. Journal of Archaeological Method and Theory. 1–52.
Morin, E., Soulier, M.-C., 2017. New criteria for the archaeological identification of bone grease processing. American Antiquity. 82, 96–122.
Munro, N.D., Bar-Oz, G., 2005. Gazelle bone fat processing in the Levantine Epipalaeolithic. Journal of Archaeological Science. 32, 223–239.
Negrino, F., Riel-Salvatore, J., 2018. From Neanderthals to Anatomically Modern Humans in Liguria (Italy): the current state of knowledge. In: Borgia, V., Cristiani, E. (Eds.), Palaeolithic Italy. Advanced Studies on Early Human Adaptations in the Apennine Peninsula. Leiden, Netherlands, pp. 159–180.
Niven, L., Steele, T.E., Rendu, W., Mallye, J.-B., McPherron, S.P., Soressi, M., Jaubert, J., Hublin, J.-J., 2012. Neandertal mobility and large-game hunting: the exploitation of reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime, France). Journal of human evolution. 63, 624–635.
O'Connell, J.F., Hawkes, K., Jones, N.B., 1988. Hadza hunting, butchering, and bone transport and their archaeological implications. Journal of Anthropological research. 113–161.
O'Connell, J.F., Hawkes, K., Jones, N.B., 1990. Reanalysis of large mammal body part transport among the Hadza. Journal of Archaeological Science. 17, 301–316.
Onoratini, G., Simon, P., 2004. Le Protoaurignacien de la grotte de l'Observatoire (Principauté de Monaco).
Outram, A., Rowley-Conwy, P., 1998. Meat and marrow utility indices for horse (Equus). Journal of Archaeological Science. 25, 839–849.
Outram, A.K., 2001. A new approach to identifying bone marrow and grease exploitation: why the "indeterminate" fragments should not be ignored. Journal of archaeological science. 28, 401–410.
Outram, A.K., Knüsel, C.J., Knight, S., Harding, A.F., 2005. Understanding complex fragmented assemblages of human and animal remains: a fully integrated approach. Journal of Archaeological Science. 32, 1699–1710.

Pike-Tay, A., Cabrera Valdés, V., Bernaldo de Quirós, F., 1999. Seasonal variations of the Middle–Upper Paleolithic transition at El Castillo, Cueva Morín and El Pendo (Cantabria, Spain). Journal of Human Evolution. 36, 283–317.

Porraz, G., Simon, P., Pasquini, A., Onoratini, G., 2010. Identité technique et comportements économiques des groupes protoaurignaciens à la grotte de l'Observatoire (Principauté de Monaco). Gallia préhistoire. 52, 33–59.

Pothier Bouchard, G., Mentzer, S.M., Riel-Salvatore, J., Hodgkins, J., Miller, C.E., Negrino, F., Wogelius, R., Buckley, M., 2019. Portable FTIR for on-site screening of archaeological bone intended for ZooMS collagen fingerprint analysis. Journal of Archaeological Science: Reports. 26, 101862.

Purdue, J.R., 1983. Epiphyseal Closure in White-Tailed Deer. The Journal of Wildlife Management. 47, 1207–1213.

Rasmussen, S.O., Birks, H.H., Blockley, S.P., Brauer, A., Hajdas, I., Hoek, W.Z., Lowe, J.J., Moreno, A., Renssen, H., Roche, D.M., others, 2014. Dating, synthesis, and interpretation of palaeoclimatic records of the Last Glacial cycle and model-data integration: advances by the INTIMATE (INTegration of Ice-core, MArine and TErrestrial records) COST Action ES0907. Quaternary Science Reviews. 106, 1–13.

Reitz, E.J., Wing, E.S., 2008. Zooarchaeology. Cambridge University Press, Cambridge.

Rendu, W., Costamagno, S., Meignen, L., Soulier, M.-C., 2012. Monospecific faunal spectra in Mousterian contexts: Implications for social behavior. Quaternary International, The Neanderthal Home: spatial and social behaviours. 247, 50–58.

Riel-Salvatore, J., 2007. The Uluzzian and the Middle-Upper Paleolithic transition in southern Italy (Ph.D.). Arizona State University, Ann Arbor, United States.

Riel-Salvatore, J., 2010. A Niche Construction Perspective on the Middle–Upper Paleolithic Transition in Italy. Journal of Archaeological Method and Theory. 17, 323–355.

Riel-Salvatore, J., Ludeke, I.C., Negrino, F., Holt, B.M., 2013. A spatial analysis of the late mousterian levels of Riparo Bombrini (Balzi Rossi, Italy). Can. J. Archaeol. 37, 70–92.

Riel-Salvatore, J., Negrino, F., 2018a. Proto-Aurignacian Lithic Technology, Mobility, and Human Niche Construction: A Case Study from Riparo Bombrini, Italy. In: Lithic Technological Organization and Paleoenvironmental Change, Studies in Human Ecology and Adaptation. Springer, Cham, pp. 163–187.

Riel-Salvatore, J., Negrino, F., 2018b. Human adaptations to climatic change in Liguria across theMiddle–Upper Paleolithic transition. In: Global Perspectives on the Impact of Drastic Environmental Changes in Hunter-Gatherer Technologies, Journal of Quaternary Science. Nuno Bicho, João Cascalheira.

Schulting, R.J., Blockley, S.M., Bocherens, H., Drucker, D., Richards, M., 2008. Stable carbon and nitrogen isotope analysis on human remains from the Early Mesolithic site of La Vergne (Charente-Maritime, France). Journal of Archaeological Science. 35, 763–772.

Sinet-Mathiot, V., Smith, G.M., Romandini, M., Wilcke, A., Peresani, M., Hublin, J.-J., Welker, F., 2019. Combining ZooMS and zooarchaeology to study Late Pleistocene hominin behaviour at Fumane (Italy). Scientific Reports. 9, 1–13.

Soulier, M.-C., 2013. Entre alimentaire et technique : l'exploitation animale aux débuts du paléolithique supérieur : stratégies de subsistance et chaînes opératoires de traitement du gibier à Isturitz, La Quina aval, Roc-de-Combe et Les Abeilles (thesis). Toulouse 2.

Soulier, M.-C., 2014. Food and technical exploitation of mammals during the early Upper Palaeolithic at Les Abeilles (Haute-Garonne, France). PALEO. Revue d'archéologie préhistorique. 287–307.

Speth, J.D., 2015. When did humans learn to boil. PaleoAnthropology. 2015, 54–67.

Stiner, M.C., 1999. Palaeolithic mollusc exploitation at Riparo Mochi (Balzi Rossi, Italy): food and ornaments from the Aurignacian through Epigravettian. Antiquity. 73, 735–754.

Stiner, M.C., 2002a. Zooarchaeological evidence for resource intensification in Algarve, southern Portugal. Promontoria, Revista do Departamento de Historia, Arqueologia e Patrimonio da Universidade do Algarve. 23–58.

Stiner, M.C., 2002b. On in situ Attrition and Vertebrate Body Part Profiles. Journal of Archaeological Science. 29, 979–991.

Stiner, M.C., Kuhn, S.L., Surovell, T.A., Goldberg, P., Meignen, L., Weiner, S., Bar-Yosef, O., 2001. Bone Preservation in Hayonim Cave (Israel): a Macroscopic and Mineralogical Study. Journal of Archaeological Science. 643–659.

Stiner, M.C., Kuhn, S.L., Weiner, S., Bar-Yosef, O., 1995. Differential burning, recrystallization, and fragmentation of archaeological bone. Journal of Archaeological Science. 22, 223–237.

Stiner, M.C., Munro, N.D., 2002. Approaches to Prehistoric Diet Breadth, Demography, and Prey Ranking Systems in Time and Space. Journal of Archaeological Method and Theory. 9, 181–214.

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The Tortoise and the Hare: Small□Game Use, the Broad□Spectrum Revolution, and Paleolithic Demography. Current Anthropology. 41, 39–79.

Tagliacozzo, A., Zeppieri, F., Fiore, I., Spinapolice, E., Del Lucchese, A., 2012. Archaeozoological evidence of subsistence strategies during the Gravettian at Riparo Mochi (Balzi Rossi, Ventimiglia, Imperia - Italy). Quaternary International, The evolution of the hominin food resource exploitation in Pleistocene Europe: Recent Studies in Zooarchaeology. 252, 142–154.

Tejero, J.-M., Grimaldi, S., 2015. Assessing bone and antler exploitation at Riparo Mochi (Balzi Rossi, Italy): implications for the characterization of the Aurignacian in South-western Europe. Journal of Archaeological Science. 61, 59–77.

Théry-Parisot, I., Costamagno, S., Brugal, J.-P., Fosse, P., Guilbert, R., 2004. The use of bone as fuel during the Palaeolithic, experimental study of bone combustible properties. 50–59.

Tomasso, A., Porraz, G., 2016. Hunter-gatherer mobility and embedded raw-material procurement strategies in the mediterranean upper paleolithic. Evolutionary Anthropology: Issues, News, and Reviews. 25, 164–174.

Trueman, C.N.G., Behrensmeyer, A.K., Tuross, N., Weiner, S., 2004. Mineralogical and compositional changes in bones exposed on soil surfaces in Amboseli National Park, Kenya: diagenetic mechanisms and the role of sediment pore fluids. Journal of Archaeological Science. 31, 721–739.

Tsanova, T., Zwyns, N., Eizenberg, L., Teyssandier, N., Le Brun-Ricalens, F., Otte, M., 2012. Le plus petit dénominateur commun : réflexion sur la variabilité des ensembles lamellaires du Paléolithique supérieur ancien d'Eurasie. Un bilan autour des exemples de Kozarnika (Est des Balkans) et Yafteh (Zagros central). L'Anthropologie, Paléolithique supérieur (I). 116, 469–509.

van der Sluis, L.G., Hollund, H.I., Buckley, M., De Louw, P.G., Rijsdijk, K.F., Kars, H., 2014. Combining histology, stable isotope analysis and ZooMS collagen fingerprinting to investigate the taphonomic history and dietary behaviour of extinct giant tortoises from the Mare aux Songes deposit on Mauritius. Palaeogeography, Palaeoclimatology, Palaeoecology. 416, 80–91.

Vehik, S.C., 1977. Bone Fragments and Bone Grease Manufacturing: A Review of their Archaeological Use and Potential. Plains Anthropologist. 22, 169–182.

Vicino, G., 1984. Lo scavo paleolitico al Riparo Bombrini (Balzi Rossi di Grimaldi, Ventimiglia). Rivista Ingauna e Intemelia. 39, 1–10.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. Journal of Human Evolution. 21, 27–48.

Weiner, S., Berna, F., Cohen, I., Shahack-Gross, R., Albert, R.M., Karkanas, P., Meignen, L., Bar-Yosef, O., 2007. Mineral Distributions in Kebara Cave. Diagenesis and its Effect on the Archaeological Record. In: Kebara Cave, Mt Carmel, Israel : The Middle and Upper Paleolithic ; Part I. American School of Prehistoric Research, Peabody Museum, Harvard University Press (Cambridge, US), pp. 131–146.

Weiner, S., Schiegl, S., Goldberg, P., Bar□Yosef, O., 1995. Mineral Assemblages in Kebara and Hayonim Caves, Israel: Excavation Strategies, Bone Preservation, and Wood Ash Remnants. Israel Journal of Chemistry. 35, 143–154.

Welker, F., 2018. Palaeoproteomics for human evolution studies. Quaternary Science Reviews. 190, 137–147.

Welker, F., Soressi, M., Rendu, W., Hublin, J.-J., Collins, M., 2015. Using ZooMS to identify fragmentary bone from the late Middle/Early Upper Palaeolithic sequence of Les Cottes, France. Journal of Archaeological Science. 54, 279–286.

Welker, F., Soressi, M.A., Roussel, M., Riemsdijk, I. van, Hublin, J.-J., Collins, M.J., 2017. Variations in glutamine deamidation for a Châtelperronian bone assemblage as measured by peptide mass fingerprinting of collagen. STAR: Science & Technology of Archaeological Research. 3, 15–27.

Wilson, G.L., 1924. The horse and the dog in Hidatsa culture. Anthropological Papers of the American Museum of Natural History. 15, 125–311.

Wißing, C., Rougier, H., Baumann, C., Comeyne, A., Crevecoeur, I., Drucker, D.G., Gaudzinski-Windheuser, S., Germonpré, M., Gómez-Olivencia, A., Krause, J., Matthies, T., Naito, Y.I., Posth, C., Semal, P., Street, M., Bocherens, H., 2019. Stable isotopes reveal patterns of diet and mobility in the last Neandertals and first modern humans in Europe. Scientific Reports. 9, 1–12.

Zeder, M.A., Lemoine, X., Payne, S., 2015. A new system for computing long-bone fusion age profiles in Sus scrofa. Journal of Archaeological Science. 55, 135–150.

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1543 **8 Supplemental information**

1544 Table S1: Peptid markers used to identify the different animal taxa in this study from

1545 Buckley et al. (2009, 2010, 2017; 2011), and Brown et al. (2016).

Taxa	2t85(A)	2t43(B)	2t45(C)	2t69(D)	1t66/67	2t41/42(E)	1t55/56(F)	2t67(G)	2t76
Herbivores									
Bos/Bison	1208.6	1427.7	1580.8	2131.1	N/A	N/A	2853.4	3033.4	
Capra	1196.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3093.4	
Cervus/Dama	1196.6	1427.7	1550.8	2131.1	N/A	N/A	2883.4	3033.4	
Capreolus	1196.6	1427.7	1550.8	2131.1	N/A	N/A	2883.4	3059.4	
Coelodonta/Diceros	1198.6	1453.7	1550.8	2145.1	N/A	N/A	2869.4	2999.4	
Equus	1198.6	1427.7	1550.8	2145.1	N/A	N/A	2883.4	2999.4	
Mammuthus	N/A	1453.7	1579.8	2115.1	N/A	N/A	2853.4	3015.4	
Ovibos	1208.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3033.4	
Rangifer	1166.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3093.4	
Rupicapra/Ovis	1196.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3033.4	
Sus	1196.6	1453.7	1550.8	2131.1	N/A	N/A	2883.3	3033.4	
Carnivores									
Alopex	1226.6	1453.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1548.8
Canis	1226.6	1453.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1576.8
Crocuta	1207.6	1453.7	1566.8	2147.1	2246.1	2808.3	2853.4	2999.4	
Gulo/Mustela/Martes	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2999.4	
Homo	1235.6	1477.8	1580.8	2115.1	N/A	2832.4	2885.4	2957.4+ 2959.4	
Lutra	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2973.4	
Lynx	1207.6	1453.7	1566.8	2163.1	N/A	N/A	2853.4	2999.4	
Meles	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2957.4	
Panthera	1207.6	1453.7	1566.8	2147.1	2216.1	2820.3	2853.4	2999.4	
Ursus	1233.7	1453.7	1566.8	2163.1	N/A	N/A	2853.4	2957.4	
Vulpes	1226.6	1437.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1548.8
Lagomorphs									
Oryctolagus	1235.6	1453.7	1566.8	2129.1	N/A	2836.3	2883.4	2957.4	
Lepus	1235.6	1453.7	1566.8	2129.1	N/A	2808.3	2883.4	2957.4	
Rodents									
Castor	1193.6	1427.7	1576.8	2129.1	N/A	N/A	2883.4	2999.4	

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1549 Table S2: Skeletal representation

Taxa	Square	Level	Skeletal portion					
			Head	Axial post-cranial	Indeterminate Limbs	Upper limbs	Lower limbs	Feet
Cervus	E1	A1_A2	1 tooth, 2 cranium frag.	2 ribs	9	2 humeri, 1 scapula	1 radius-ulna, 1 metacarpal	1 tarsal or carpal
	D1	A1_A2	1 cranium frag.		4			
	AA1	A1			1			
	DD1	A1		1 rib	2			
	DD1	A2			2			
	FF3	A2		1 rib				
Total *Cervus*			4	4	18	3	2	1
Capra	E1	A1_A2		1 rib	6		1 metacarpal	
	D1	A1_A2			2		1 radius-ulna	
	DD1	A1			1			
	DD1	A2	1 tooth					
	EE1	A2	1 tooth					
	FF3	A2			1			
Total *Capra*			2	1	10		2	
Bos_Bison	E1	A1_A2	1 cranium frag.	1 rib	9			
	D1	A1_A2			4			
	DD1	A1			5			
	DD1	A2	1 tooth		1			
	EE1	A2			1			
	EE1	A1	1 tooth					
Total *Bos_Bison*			3	1	20			
Equus	FF3	A1					1 hamatum	
	FF3	A2					1 lunate	

	E1	A1_A2	1 tooth		1	1 femur	
	DD1	A2	1 tooth			2 tibiae	
Total *Equus*			2		1	3	2
Sus	E1	A1_A2	1 tooth				
	CC1	A2	2 teeth				1 phalanx
	DD1	A1	1 tooth				
	FF3	A2					1 phalanx
Total *Sus*			5				2
Cervid	E1	A1_A2	1 antler		3		1 phalanx
	D1	A1_A2	1 cranium frag., 1 tooth				
	CC1	A1	1 tooth				
	DD1	A2	1 antler, 2 teeth				
	DD1	A1		1 rib			
	EE3	A2		1 rib	1	1 femur	
	FF3	A2			2		
Total Cervid			7	2	6	1	1

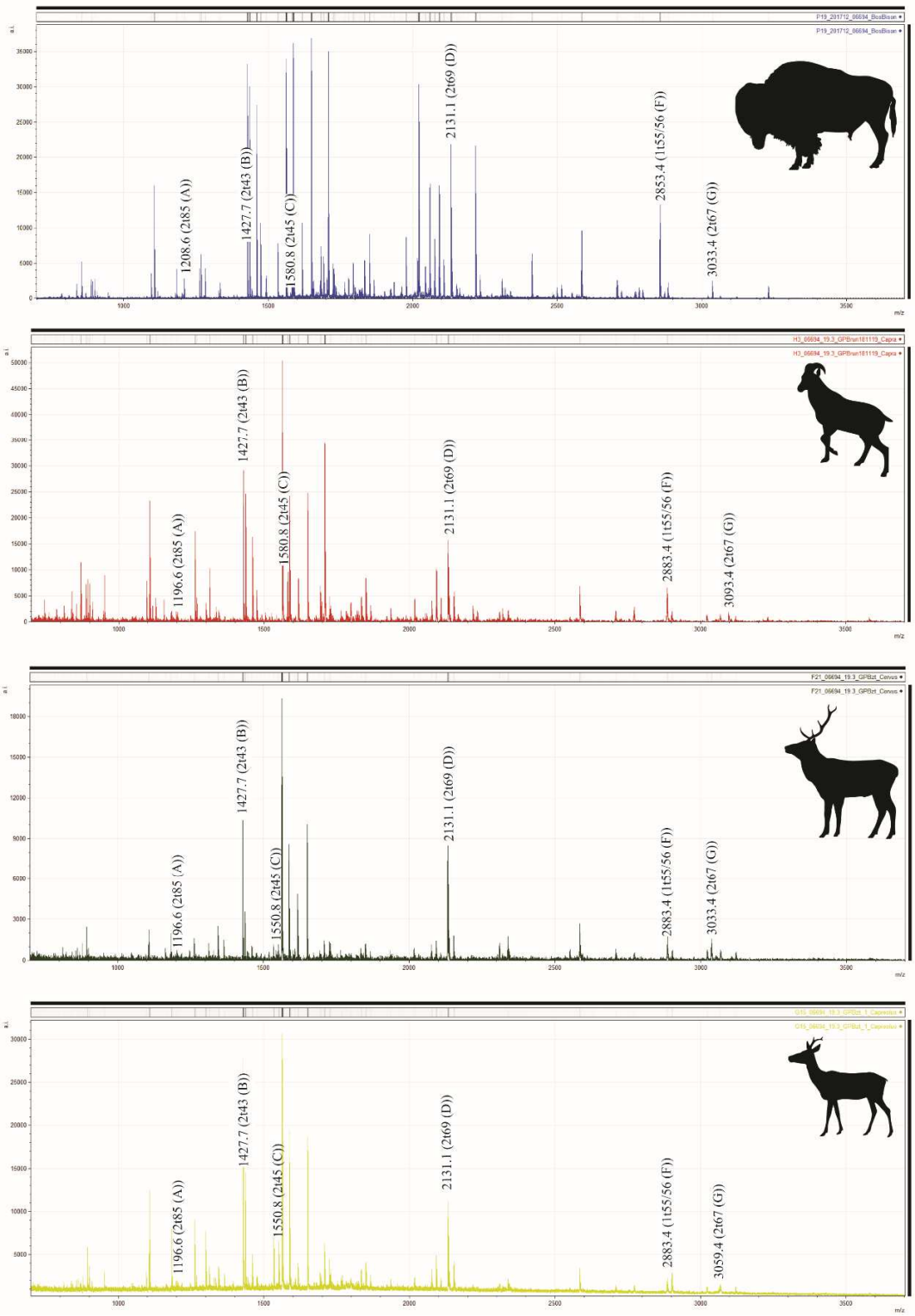
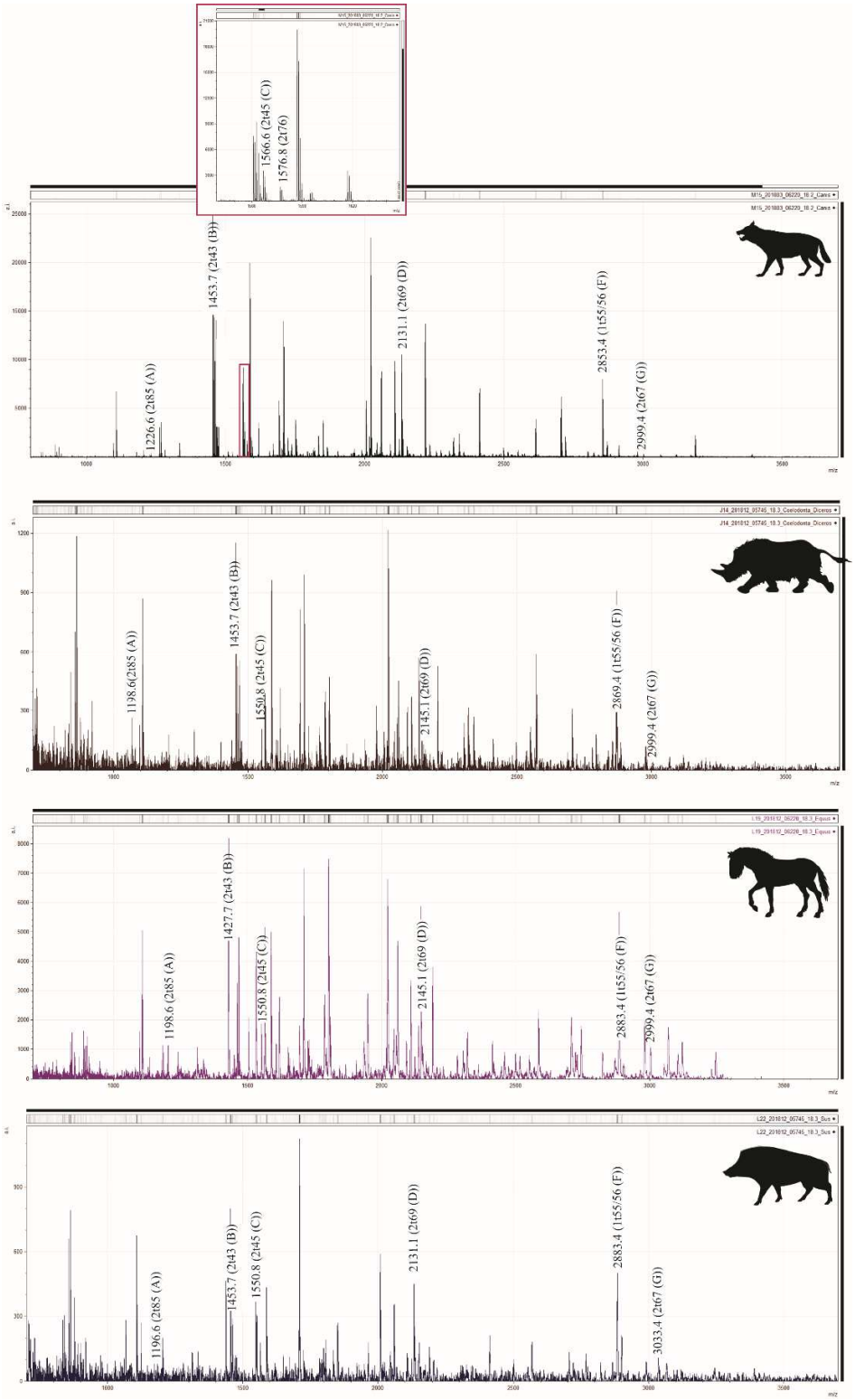
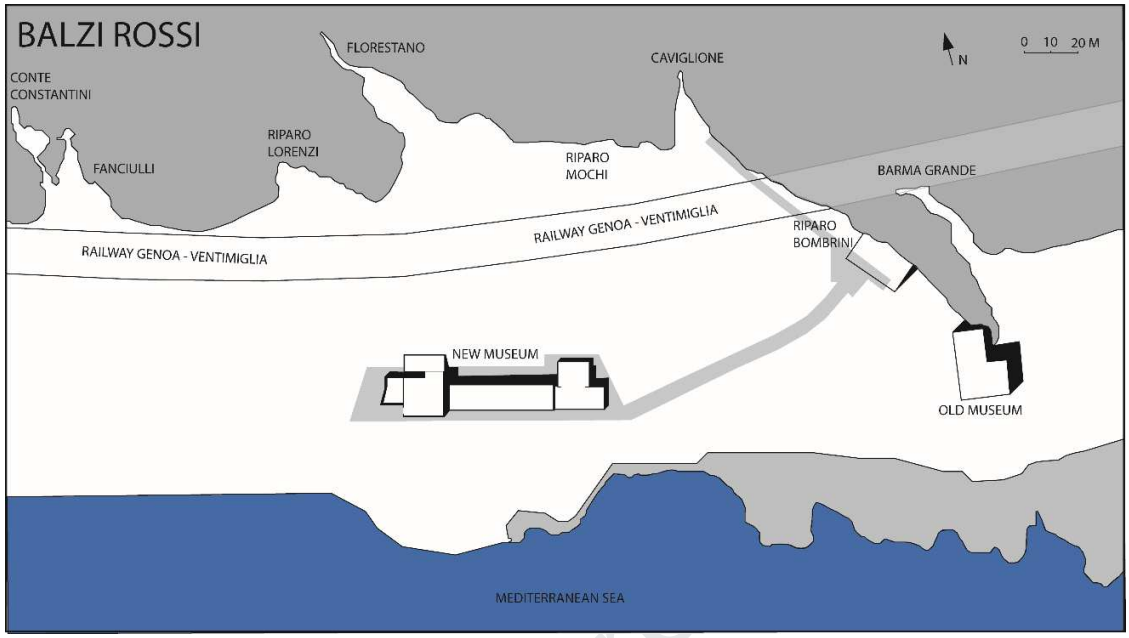


Figure S1: Examples ZooMS spectra from Bombrini corresponding starting from above to: *Bos/Bison*, *Capra*, *Cervus*, and *Capreolus*. Animal silhouette images from http://phylopic.org/.



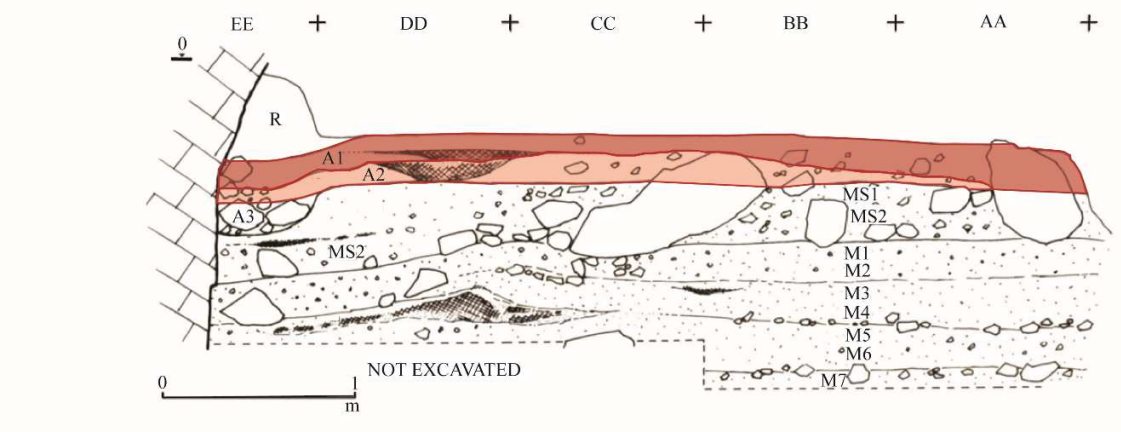
1553 Figure S2: Examples ZooMS spectra from Bombrini corresponding starting from above
1554 to: *Canis*, *Coelodonta/Diceros*, *Equus*, and *Sus*. Animal silhouette images from
1555 http://phylopic.org/.

1556 **Figures mentioned in the text**



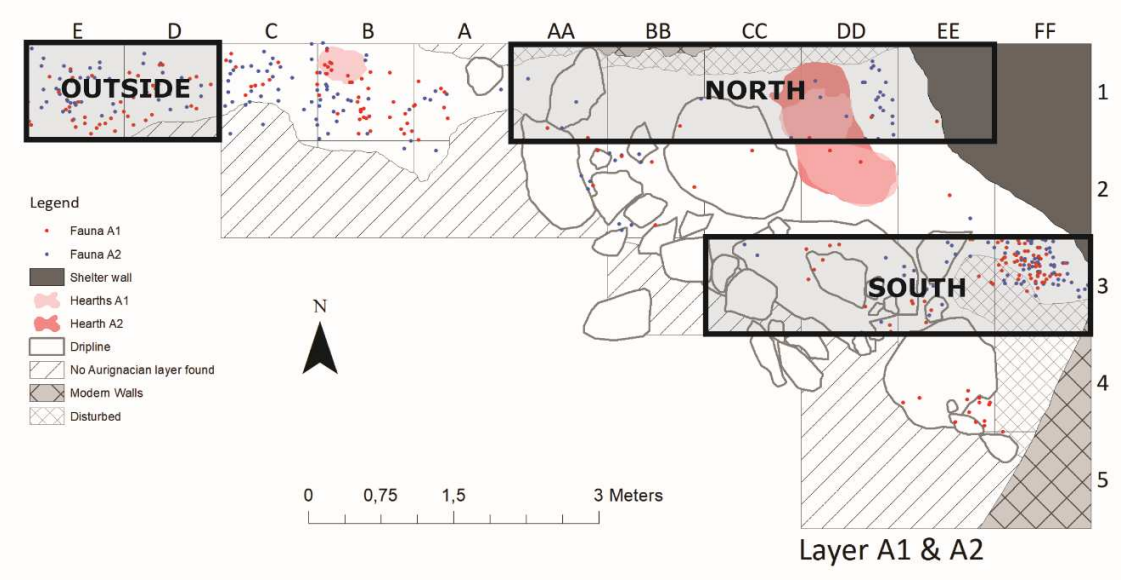
1557 Figure 1: Map of the Balzi Rossi cave complex (Ventimiglia, Italy) showing
1558 archaeological sites, including Riparo Bombrini, Riparo Mochi, and Grotta del
1559 Caviglione mentioned in the text.

1560



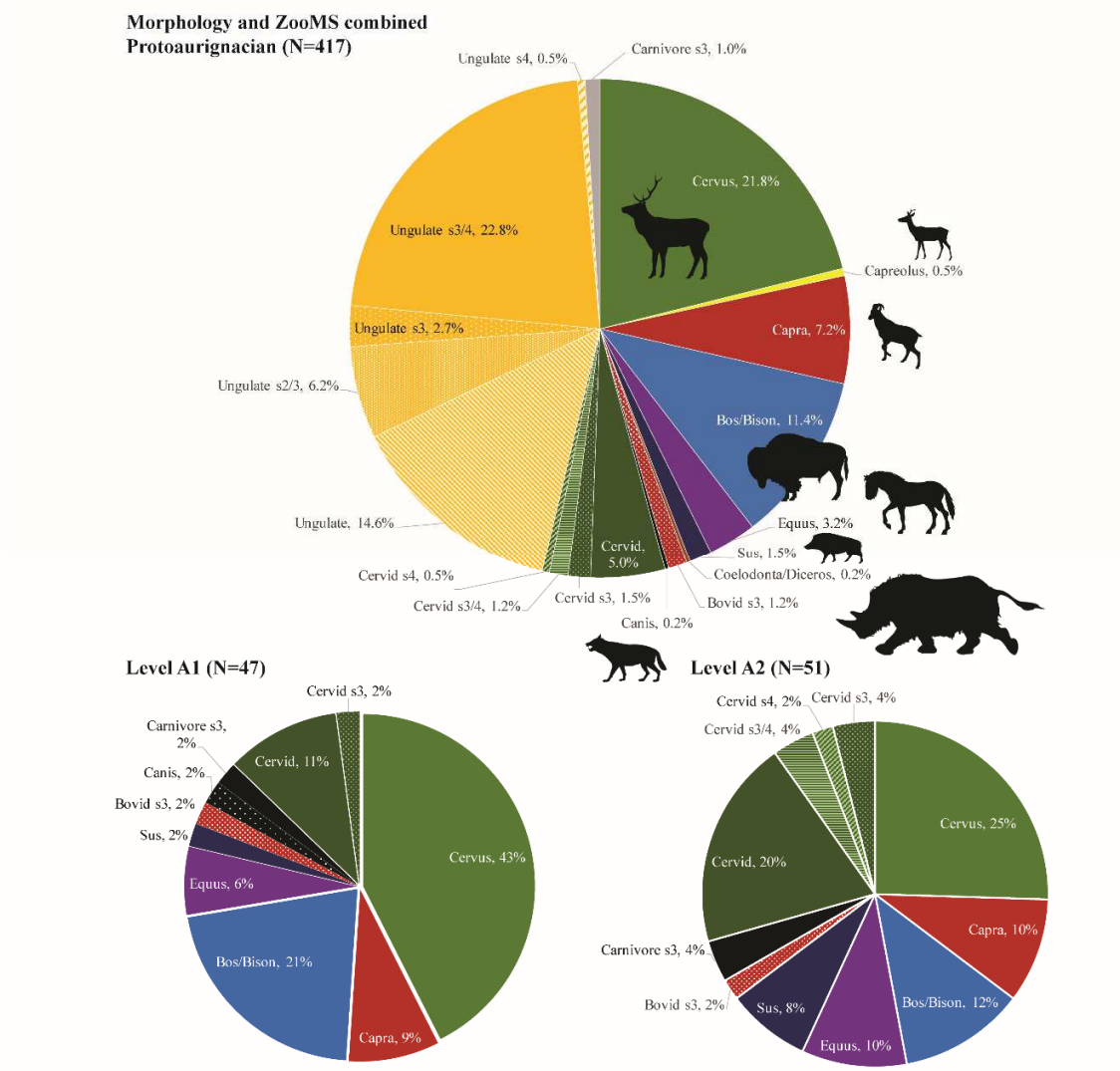
1561 Figure 2: Stratigraphy of Riparo Bombrini showing Protoaurignacian levels A1 and A2.

1562



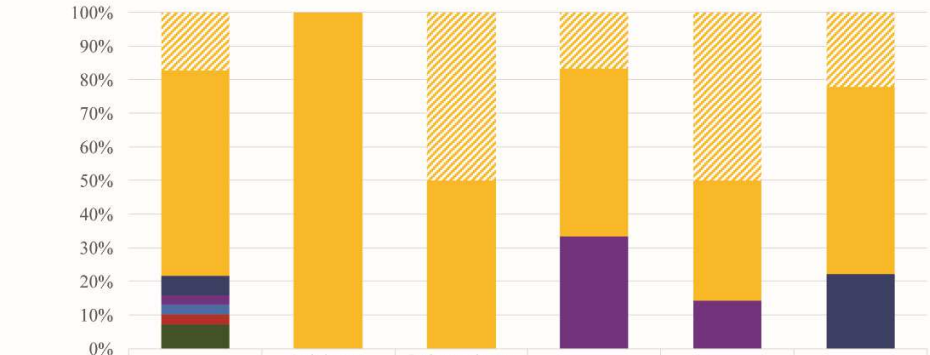
1563 Figure 3: Faunal distribution map combining plotted finds from levels A1 and A2 at
1564 Riparo Bombrini, showing the three selected areas in this study: north, south, and outside.

1565
1566



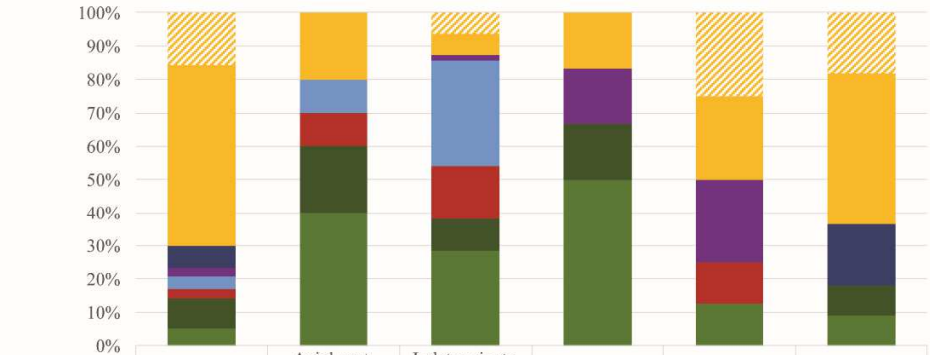
1567 Figure 4: Pie charts showing total NISP for level A1 and A2 (upper), NISP of level A1
1568 (lower left), and A2 (lower right) both excluding the “Ungulate” categories. Animal
1569 silhouette images from http://phylopic.org/.
1570

Skeletal representation with morphology



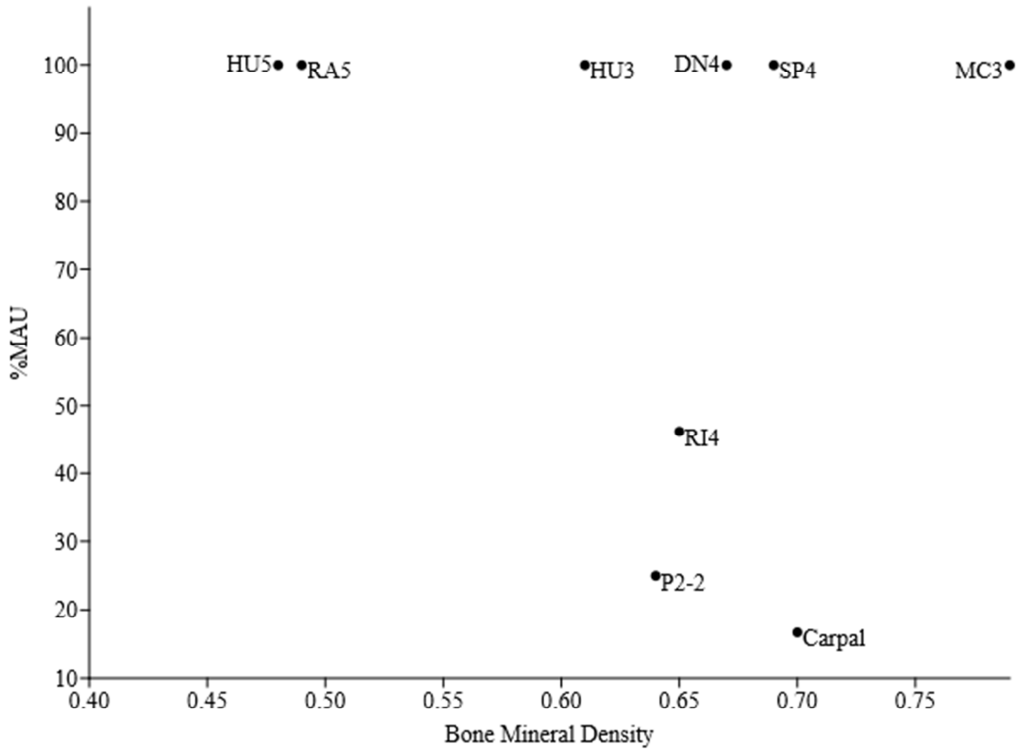
	Head	Axial post-cranial	Indeterminate limb	Upper limb	Lower limb	Foot
Ungulate s2/3	12	0	4	1	7	2
Ungulate s3/4	42	2	4	3	5	5
Sus	4	0	0	0	0	2
Equus	2	0	0	2	2	0
Bos/Bison	2	0	0	0	0	0
Capra	2	0	0	0	0	0
Cervus	0	0	0	0	0	0
Cervid	5	0	0	0	0	0

Skeletal representation with morphology and ZooMS



	Head	Axial post-cranial	Indeterminate limb	Upper limb	Lower limb	Foot
Ungulate s2/3	12	0	4	0	4	2
Ungulate s3/4	42	2	4	1	4	5
Sus	5	0	0	0	0	2
Equus	2	0	1	1	4	0
Bos/Bison	3	1	20	0	0	0
Capra	2	1	10	0	2	0
Cervid	7	2	6	1	0	1
Cervus	4	4	18	3	2	1

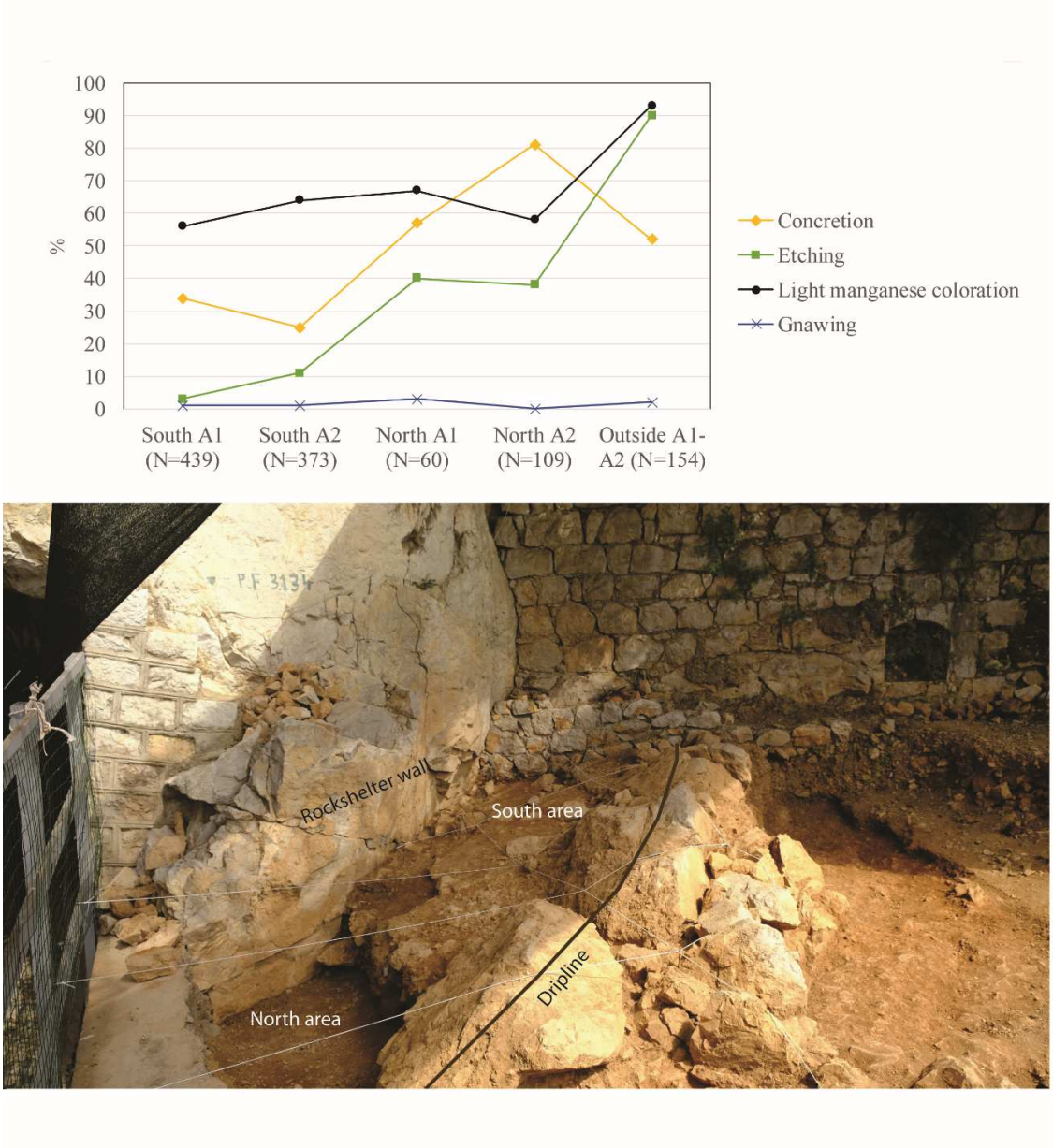
1571 Figure 5: Skeletal representation of the identified taxa from combined levels A1 and A2
1572 at Riparo Bombrini.



1573

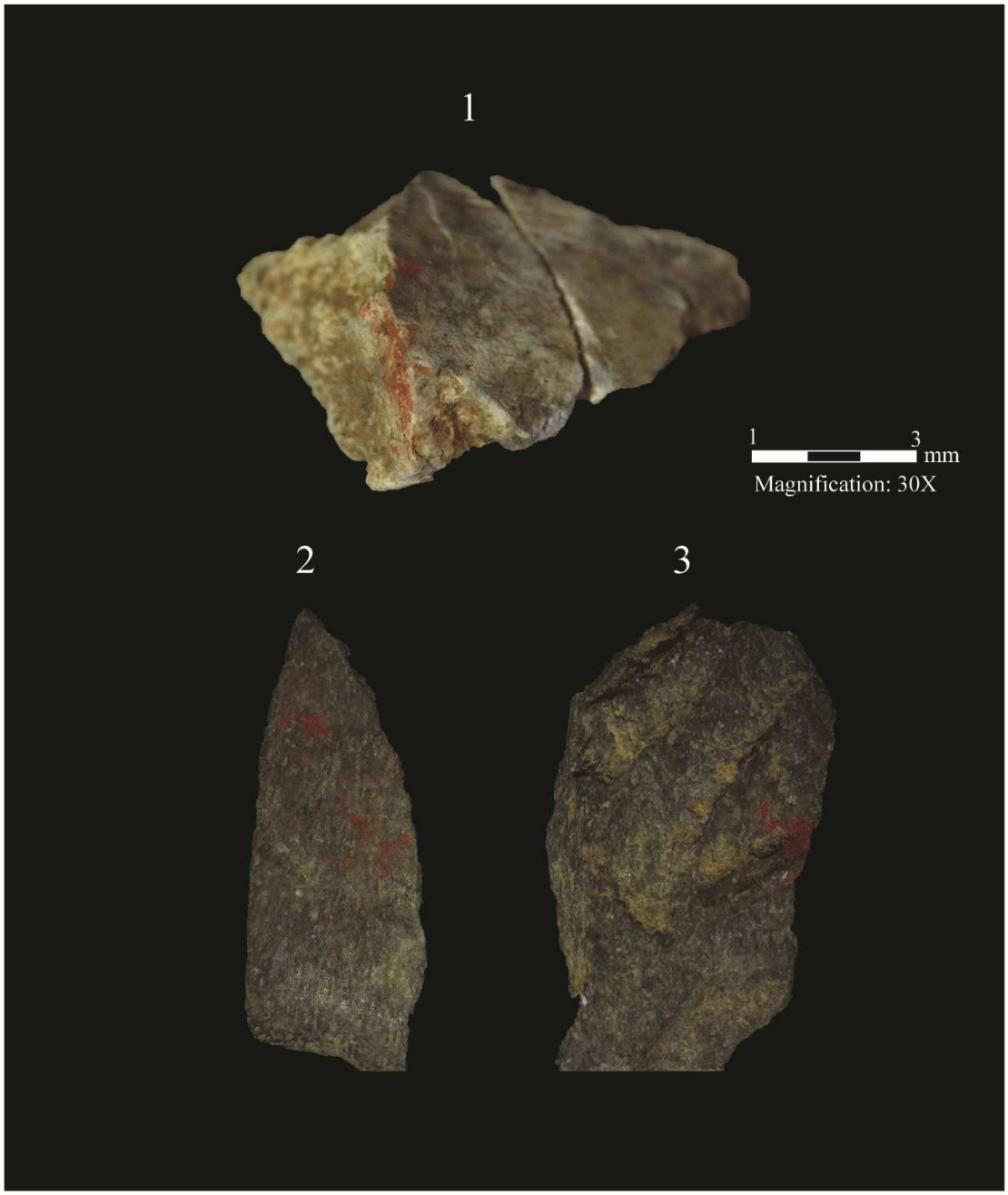
1574 Figure 6: Relationship between %MAU of cervids and bone mineral density. All density
1575 scan sites are detailed Lam et al. (1999): *HU* humerus, *RA* radius, *DN* mandible, *SP*
1576 scapula, *MC* metacarpal, *RI* rib, *P2* second phalanx.
1577

1578 Figure 7: Number of bone fragments for each size categories excluding teeth (upper), and
1579 normalised proportion of the same set of bone fragments in each size categories using
1580 LOG 10 (lower).



1581 Figure 8: Proportion of taphonomic effects (concretion, etching, manganese, and
1582 carnivore gnawing) on long bone shafts within each Protoaurignacian levels (A1 and A2)
1583 and site areas (south, north, and outside) (above), site contextualisation showing north
1584 and south areas delimited by the original rockshelter wall and the dripline.
1585

Figure 9: Example of anthropic marks: (1) grooving, (2) needle tip, (3) bone flake, magnification 20X, scale = 3 mm.



1590 Figure 10: Example of calcined (1) and carbonized (2, 3) bone fragments covered with
1591 dots of red ochre, magnification 30X, scale=3mm.
1592
1593

1594 Figure 11: Proportion of six bone types in relation with six size classes within each level
1595 (A1 and A2) and site areas (south, north, and outside) excluding the part and whole
1596 anatomical elements.
1597
1598

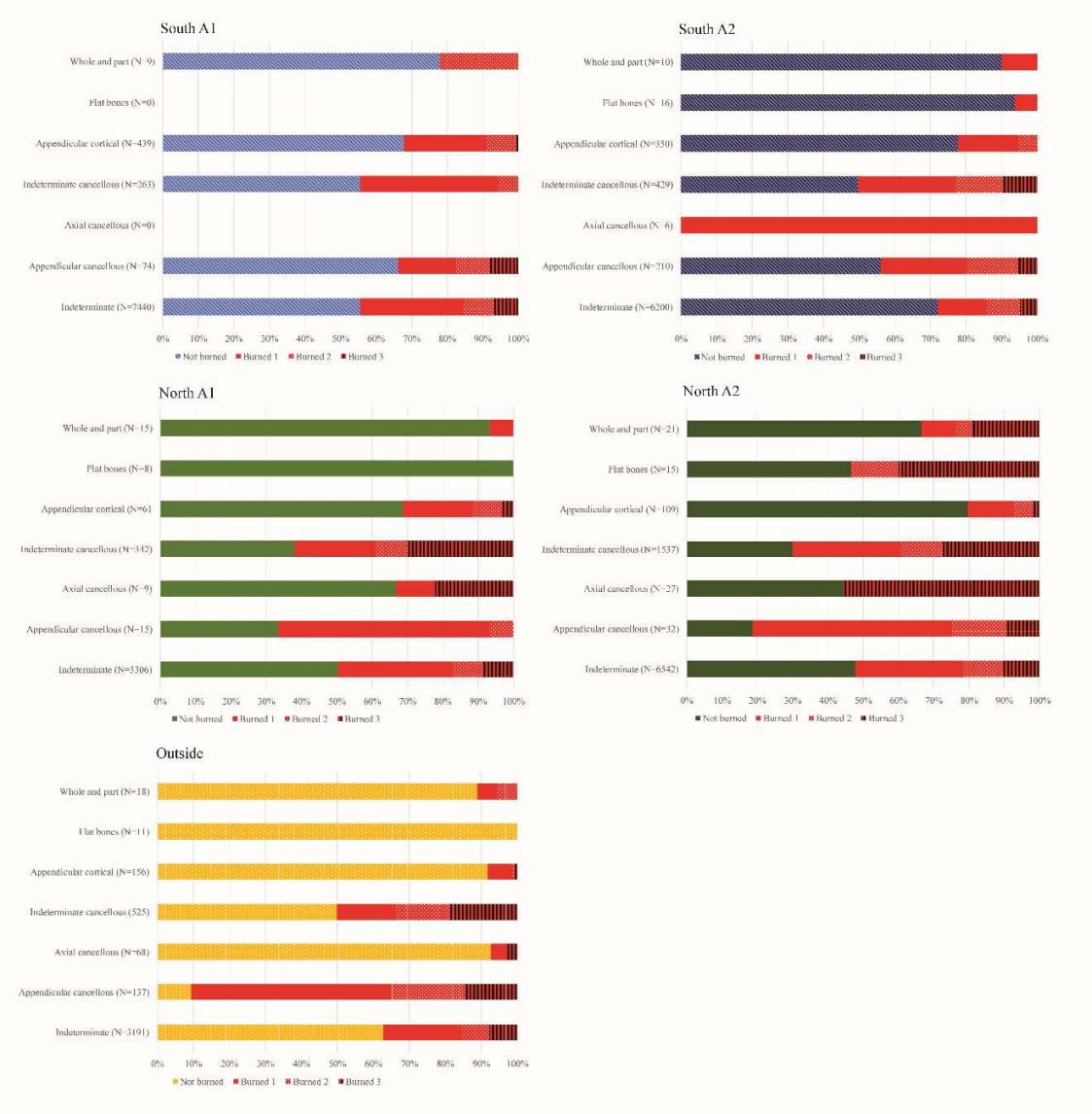
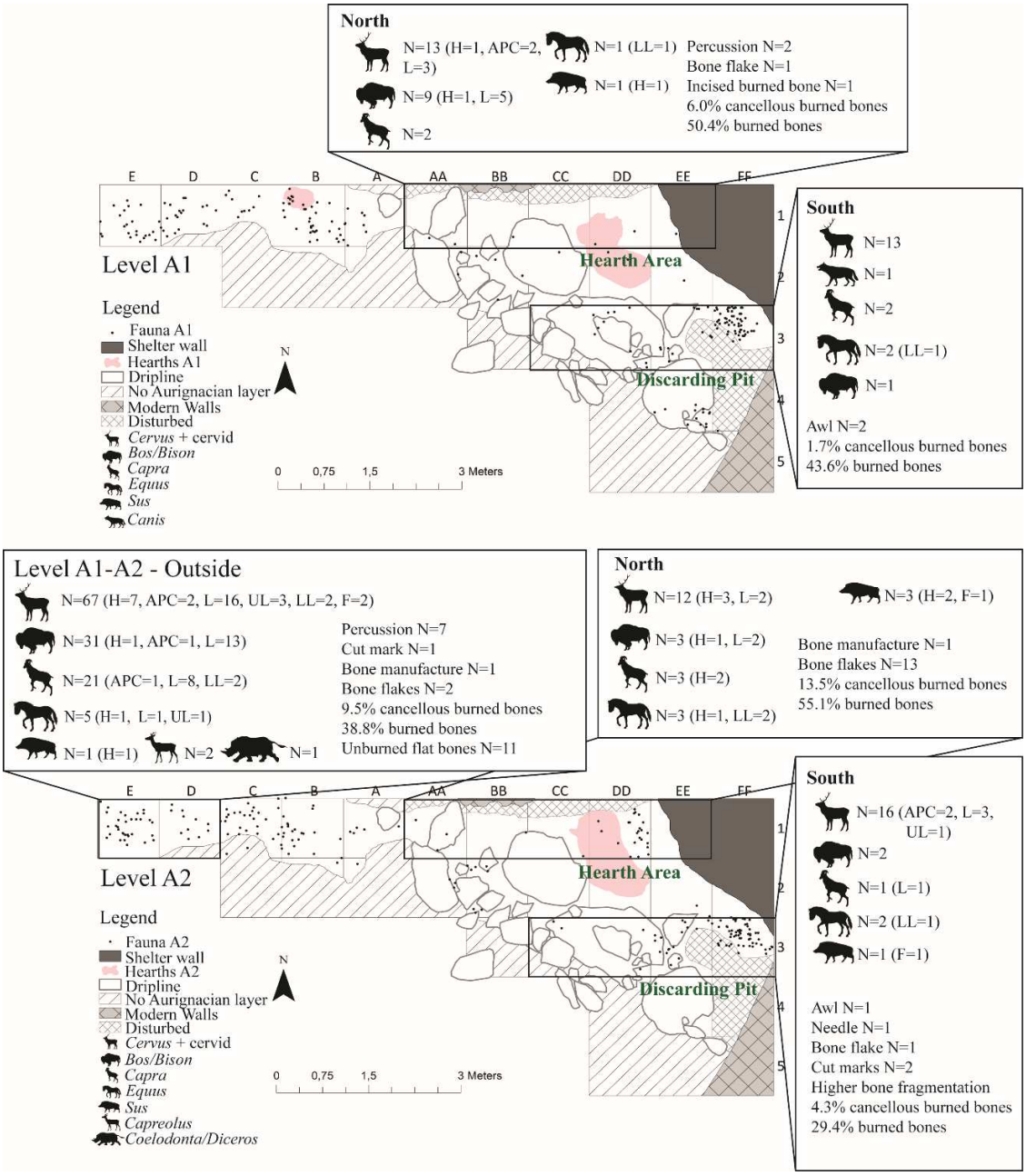


Figure 12: Proportions of burned (burned 1, burned 2, burned 3) and unburned bones in relation with seven bone type categories within each level (A1 and A2) and site areas (south, north, outside).



1604 Figure 13: Distribution maps (level A1: top, level A2: bottom) of all plotted faunal
1605 remains with summarised archaeozoological data, including NISP and skeletal
1606 representation (*H* head, *APC* axial post cranial, *L* limb, *UP* upper limb, *LL* lower limb, *F*
1607 foot), and anthropic taphonomic data within each site area (south, north, and outside).
1608 Animal silhouette images from http://phylopic.org/.

1609
1610

Tables mentioned in the text

Table 1: NISP results combining levels A1 and A2 and separately showing taxa identified with morphology, with ZooMS, and with the combined data.

Taxa	Morphology	ZooMS	Combined
Cervus	0	88	88
Capreolus	0	2	2
Capra	2	27	29
Bos/Bison	2	44	46
Equus	6	7	13
Sus	6	1 (already morphologically identifiable)	6
*Bovid size 3**	5	0	5
Coelodonta/Diceros	0	1	1
Canis	0	1	1
Cervid	0	20	20
Cervid size 3	1	5	6
Cervid size 3/4	2	3	5
Cervid size 4	2	0	2
Ungulate	34	25	59
Ungulate size 2/3	29	0	25**
Ungulate size 3	9	2	11
Ungulate size 3/4	88	9	92**
Ungulate size 4	2	0	2
Carnivore size 3	4	0	4
Poor collagen	n/a	409	n/a
Indeterminate	32156 (99.4%)	n/a	31931 (98.7%)
Total	**32348**	**644**	**32348**

*Animal size categories are adapted from Brain (1981).

**Some of the bone fragments from this category were identified to a more precise (e.g. a "ungulate size 3/4" further identified with ZooMS to a "*Cervus*" category).

1618 Table 2: Age determinations

Taxa	Square	Level	Fetal	Juvenile	Adult	Old	Element	Tooth wear stage*	Height (mm)
NID	E1	A1_A2	2				Indeterminate		
	DD1	A2	1				Indeterminate		
	EE1	A2	2				Indeterminate		
	EE3	A2	1				Indeterminate		
	FF3	A1_A2	1				Indeterminate		
Sus	FF3	A2		1			phalanx fusing		
	E1	A1_A2		1			molar or premolar	stage 1	
	DD1	A1_A2				1	premolar	stage 5	
Cervid	E1	A1_A2		1			phalanx unfused		
	D1	A1_A2		1			decidual premolar 4	stage 3	
	DD1	A2			1		upper molar	stage 4	9
Capra	EE1	A2		1			decidual premolar 4	stage 2	
Bos_Bison	DD1	A2			1		upper molar	stage 3	
	EE1	A1			1		lower molar	stage 3	23.7

1619 *Gross stage estimation: stage 0 = unworn, stage 1= slightly worn, stage 2= worn, stage 3
1620 = very worn, stage 4 = extremely worn.
1621

1622

1623 Table 3: Summary of taphonomic data within each Protoaurignacian levels (A1 and A2)
1624 and site areas (south, north, and outside).

	South A1	**South A2**	**North A1**	**North A2**	**Outside A1-A2**
Mean FFI score	5.94	5.74	5.43	4.84	4.47
ZooMS success rate	18.7% (N=134)	29.2% (N=89)	26.7% (N=90)	9.4% (N=128)	77.8% (N=171)
Anthropic percussion (N)	0	0	2	0	7
Cut marks (N)	0	2	0	0	1
Ochred bones (N)	0	0	1	92	0
Flakes (N)	0	1	1	13	2
Bone manufacture (N)	0	0	0	1	1
Bone tools (N)	2 awl fragments*	1 needle tip, 1 awl*	0	0	0
Decorative elements (N)	0	0	1 incised bird diaphysis*	0	0
Proportion of total burned bones (%)	43.6% (N=8225)	29.4% (N=7221)	50.4% (N=3756)	55.1% (N=8283)	38.8% (N=4106)
Proportion of cancellous burned bones (%)	1.7% (N=8225)	4.3% (N=7221)	6.0% (N=3756)	13.5% (N=8283)	9.5% (N=4106)
Proportion of cancellous bones (burned and unburned combined) (%)	4.1% (N=8225)	8.9% (N=7221)	9.7% (N=3756)	19.3% (N=8283)	17.8% (N=4106)

1625 *Previously published (Holt et al., 2019)

1626

Table 4: Comparison of the organisational strategies employed in levels A1 and A2 at Riparo Bombrini as described in Riel-Salvatore and Negrino (2018a, 2018b) and added information from the faunal and spatial data.

Previously observed behaviors in the Protoaurignacian levels at Riparo Bombrini	
Continuous dominance of bladelets	
Same *Chaîne opératoire* to produce bladelets: flexible technocomplex	
Level A1: Residential mobility	Level A2: Logistical mobility
Warmer climate*	**Colder climate***
Shorter occupations of the base camp	**Resilience through HE4**
↑ Curated lithic organization	Longer occupations of the base camp
↑ Retooling	↑ Cores and unbroken bladelets
Stouter, but shorter bladelets	Longer, narrower bladelets
Focus on local raw material	↑ exotic raw material
Additional observations made from the faunal and spatial data	
Continuous faunal diversity: generalist hunting strategies close to the site	
Continuous occupation of the base camp with distinct areas of domestic activities	
Less defined faunal aggregations	↑ aggregation of faunal remains
Less systematic use of bones as fuel	↑ bone flakes and faunal concentration next to the hearth
	↑ proportion of burned cancellous bones
	Seasonal occupations

*Combined data from microfauna, pollen, and macrofauna in Holt et al. (2019), and Riel-Salvatore and Negrino (2018a).

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We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us. We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

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